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A NOVEL MEASURE OF PROTECTED AREA ISOLATION: CORRELATIONS WITH THE PROTECTION STATUS AND SURROUNDING LAND-USE INTENSITY

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AVANT-PROPOS

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TABLE DES MATIÈRES

LISTE DES FIGURES

Figure Page

LISTE DES TABLEAUX

Tableau Page

RÉSUMÉ

La terre compte 110 000 aires protégées (AP) couvrant 12% de sa surface. Or, les AP ne parviennent pas à maintenir l'intégrité écologique telle que précédemment envisagée et le taux d'extinction des espèces se maintient à un rythme alarmant même à l'intérieur des réserves. Des études récentes suggèrent que l'altération des terres entourant les AP influe sur la biodiversité et les fonctions des écosystèmes à l'intérieur des AP. Une façon de quantifier le contraste entre l'intérieur et l'extérieur des AP est donc requise afin d'évaluer l'efficacité du réseau mondial d'AP et l'améliorer. Nous avons développé une mesure de contraste d'habitat basé sur un indice de végétation comparant le couvert végétal à l'intérieur et à l'extérieur des AP mesurée à partir d'images satellitaires (résolution 500 m^2). La mesure a été appliquée à un échantillon des AP mondiales. Le contraste entre la contagion (l'hétérogénéité du couvert végétal) à l'intérieur et à l'extérieur des AP était significatif pour la grande majorité des AP analysées, avec l'intérieur des AP présentant un couvert végétal plus uniforme que les terres environnantes. Contrairement aux études précédentes, nous avons trouvé un effet important du niveau de protection IUCN des AP et le niveau de contraste, celui-ci étant significativement plus élevé dans les AP à niveau de protection élevé que faible. Les réserves avec un haut niveau de protection sont généralement éloignées, mais sont néanmoins généralement situées dans des régions hautement influencées par des activités agricoles et forestières. Les AP avec un bas niveau de protection sont, elles, localisées plus près des zones fortement peuplées et sur des terres plus productives. La mesure de contagion développée dans cette étude permet d'évaluer rapidement l'état des AP à grandes échelles et dans différents biomes.

Mots clefs: aire protégée, complexité, analyse spatiale, ndvi

ABSTRACT

Protected areas cover over 12% of the terrestrial surface of Earth, and yet many are failing to protect species and ecological processes as originally envisioned. Recent studies suggest that an important reason for this failure is an increasing contrast between the protected lands and the surrounding matrix of often highly-altered landcover. This contrast increases the effective distance between the protected area and other natural areas, which makes it more and more difficult for animals to move among them and for ecological processes to operate between them. We measured the isolation of 114 protected areas distributed worldwide by comparing the landcover heterogeneity inside the protected areas to landcover heterogeneity outside their borders. We quantified heterogeneity as the "contagion" of greenness measured from NDVI (Normalized Difference Vegetation Index) values, where a higher value of contagion indicates less heterogeneous landcover. We then measured isolation as the difference between mean contagion inside the protected area and within three buffers at increasing distances from the protected area borders. The isolation of protected areas was significantly positive in 110 of the 114 protected areas, indicating that landcover is consistently more heterogeneous 10-20km outside a protected area than inside its borders. Unlike previous studies, we found that sites with higher IUCN protection status were more isolated (i.e. showed higher contrast in heterogeneity inside vs. outside the protected area) than were protected areas with lower IUCN protection status. Our study provides a novel way to assess the isolation of protected areas in different environmental contexts and regions.

Keywords: parks, reserves, landcover heterogeneity, fragmentation, landscape matrix, complexity, HANPP, IUCN, NDV

INTRODUCTION GÉNÉRALE

Problématique

In the current era of unprecedented species extinction rates, with habitat alteration being the primary cause (Joppa et al. 2008), protected areas (PA) remain the key conservation strategy towards slowing the current loss of global biodiversity. The World Conservation Union definition of a PA (UNEP 2009) is a piece of the earth regulated for preserving ecological integrity. Ecological integrity in this context is the ability of an ecosystem to maintain a community of organisms that has species composition, diversity, and functional organization comparable to those of natural habitats (Karr & Dudley 1981).

Recent decades have seen an explosion of protected lands and there are now over 110 000 terrestrial PAs worldwide, covering over 12% of the Earth's land surface. However, PAs are not maintaining ecological integrity as originally envisioned (Hansen & DeFries 2007). Despite adequate protection, in terms of the efficacy of basic management activities and policy enforcement in PAs, alarming species extinction rates persist even in set-aside reserves (Bruner et al. 2001; DeFries et al. 2005). A growing body of research acknowledges that the fundamental reason PAs are failing is an increasing discontinuity between the protected habitats and the surrounding matrix of, often highly altered, landcover (DeFries et al. 2005; DeFries et al. 2007; Harcourt et al. 2001; Newmark 2008). Thus, the effectiveness of PAs depends on processes operating both outside and inside their borders. Empirical and theoretical analyses suggest that PA isolation arises from either a biased localization away from biophysically well-suited habitats towards more extreme geographical settings (e.g. cold, dry, high altitude, low productivity, topographically complex settings) or intensifying

landcover alteration around PAs (Hansen & DeFries 2007; Hansen & Rotella 2002; Scott et al. 2001).

Several studies have equated human density, landcover alteration, hunting, and small reserve size to forms of PA isolation (Bruner et al. 2001; DeFries et al. 2007; Newmark 1995; Peres 2005). Furthermore, studies have shown strong positive correlations between species extinctions and such forms of PA isolation (Newmark 2008; Parks & Harcourt 2002). For example, DeFries' et al. (2005) Vegetation Continuous Fields product, a measure of forest cover loss, indicated that nearly 70% of the PA buffers (IUCN management category I & II) experienced habitat loss over the last 20 years in moist and dry tropical forests.

Clearly, the nature of the landcover matrix surrounding PAs is crucial to maintaining conservation priorities (Franklin & Lindenmayer 2009), yet there are few standardized methods that compare PAs embedded into different environmental and socio-economical contexts or measure relative habitat change across PA borders. In fact, to date there have been no published attempts to accomplish both of these objectives at the global scale.

Here I present a comparison of the landcover matrix inside PAs to the surrounding matrix outside their borders using the contagion metric of spatiotemporal NDVI values (Normalized Difference Vegetation Index). The objective of this study is to explore the question: how isolated are different PAs of the world in their landscape pattern of vegetation heterogeneity and what are the common factors of their isolation?

État des connaissances

Increasing Isolation of PAs

Recent studies indicate that land use intensity has greatly increased over the past few decades in the lands surrounding PAs (Brooks et al. 2002; DeFries et al. 2005; Joppa et al. 2008; Oliveira et al. 2007). Oliveira, Asner et al. (2007) measured leakage from newly created forest concessions. They showed that restricting land-use reduced deforestation within the concession areas, but dramatically increased it in the surrounding areas.

DeFries et al. (2005) used multiple sources of satellite data to estimate the extent of forest and habitat loss due to deforestation over the last 20 years within and surrounding 198 of the most highly protected areas (IUCN status 1 and 2) located throughout the world's tropical forests. They found that nearly 70% of PAs in their sample experienced loss of forest cover within a 50 km periphery and, while loss of habitat occurred in all tropical regions, PAs in South and Southeast Asia were most severely affected.

Joppa et al. (2008) measured the percentage of natural forest cover inside and outside PAs in four tropical moist forest regions based on a categorized 1-km^2 resolution landcover product. They found that PAs in the Atlantic Coast forest and West Africa regions had sharp boundaries in forest cover at their edges and that forest fragmentation was particularly high surrounding small PAs. On the other hand, PAs in more remote regions of the world such as the Congo and parts of the Amazon displayed little change in percent of natural forest cover from inside PAs to outside their boundaries (up to 28 km). However, in these regions deemed more remote, PAs were often part of a network of reserves and thus their surroundings often included other PAs and hence little

change in forest cover. Moreover, categorized landcover products at relatively large spatial resolutions may overestimate forest cover. Categories classified as 'natural forest cover' are quite liberal and may include alternate vegetation cover types (i.e. plantations or forests that have been cut partially or selectively). Nonetheless, viewed conservatively, Joppa's et al. (2008) study suggests that in some regions a large number of the world's PAs are highly isolated in terms of landcover discontinuity between their interior and their surroundings.

Ecological Linkages: effects of PA isolation

The presumption that PA isolation compromises their conservation efficacy has been supported by the findings of Bruner et al. (2001) and Hansen et al. (2005) and others. For example, 11 of 13 national parks in the western United States have lost large mammal species since park establishment, with 5-21.4% of original species lost (Parks and Harcourt 2002). Climate change is undoubtedly altering critical ecological processes (fire, flooding, growth patterns, exotic species invasions, and pest and pathogen dynamics). However, a major reason PAs are not functioning well, and perhaps cumulative with climate change impacts, may be that human land use is expanding and intensifying on surrounding lands. This may result in changes in ecological function and biodiversity within PAs.

Reserve size has been a highly discussed and analyzed component of PAs and their design since the reserve dichotomy of 'single large or several small' was presented (Burkey 1989). Numerous studies have suggested that small reserves are often highly impacted by increased anthropogenic landuse (Brashares et al. 2001; Buechner 1987; DeFries et al. 2005; Harcourt et al. 2001). Since small PAs are often part of larger ecosystems and they are heavily

influenced by human impacts outside their boundaries, they can highlight the potential threats of PA isolation and identify important ecological linkages between PAs and their surroundings. As such, PA isolation effects that studies have identified in small PAs may be the fate of larger ones if land use intensity, hence isolation, continues to increase around PAs of any size. On the other hand, human density in PA surroundings can surmount any size-dependant effects of PA isolation. For example, extinction rates of large mammals in national parks of the western United States correlated more strongly with local human density than they did with park size (Parks and Harcourt 2002).

Still, the size of PAs has been related to species losses, with smaller (more isolated) PAs having significantly more problems of species loss than larger ones (Brashares et al. 2001; Maiorano et al. 2008; Newmark 1995; Peres 2005; Woodroffe & Ginsberg 1998). In Brashares et al. (2001), extinction rates for 41 species of large mammals in six nature reserves in West Africa were 14-307 times higher than those predicted by models based on reserve size alone. Human population (within 50 km of PAs) and reserve size accounted for 98% of the observed variation in extinction rates between reserves. Likewise, Newmark (1987) found similar results using the post-establishment loss of mammalian species in 14 western north American parks. Only the largest park (21 000 km^2) still contained an intact historical mammalian faunal assemblage and was able to maintain populations independent of its surroundings. The natural post establishment loss of mammalian species was most likely attributable to the loss of habitat and the active elimination of fauna on adjacent lands or what has been described as short-term insularization effects. The loss of habitat on lands adjacent to PAs has a twofold effect: it increases the probability of local species extinctions because smaller parks have smaller populations and, thus, a higher probability of extinction; and the disturbance reduces the potential for colonization from adjacent lands (i.e., parks are population sinks and adjacent

lands are population sources, traits which are especially evident in small reserves).

The disparities between land protection and both loss of species and faltering system functioning in PAs has also been attributed to their non-random location (Hansen & Rotella 2001). This factor may also occur and act in concert with size-dependant isolation effects, posing ecological threats to PAs. Harcourt et al. (2001) found that small reserves in Africa are significantly more likely to be located in regions of high human density and are especially likely to lose species. Moreover, Rivard et al. (2000) found that extinction rates of mammals in Canadian national parks were associated both with park area and with the extent of intense land use outside of parks.

Expanding and intensifying land use in habitat outside PAs reduces the effective size of the PA and creates increasing isolation. Gallopin (2006) noted that urban populations have the capacity to alter ecosystems more than 100 km away. For example, declines of several large-mammal species in Kenyan parks over the past 30 years were statistically associated with human use factors and land use intensification in the wet-season habitats outside of the PA boundaries (Hansen and DeFries 2007). In a meta-analysis, Hansen and DeFries (2007) reviewed research and theory in spatial ecology, island biogeography, metapopulations and some plant and animal distributions in PAs to outline ecological mechanisms that link PAs to surrounding lands. The central conclusion made was that PAs are often parts of larger ecosystems and that land use change in the unprotected portion of the ecosystem may rescale the ecosystem, leading to changes in essential ecological processes and biodiversity within the reserve. They outlined four general mechanisms by which land use surrounding PAs alters ecological function within: effective size of the ecosystem, flows of ecological process zones, crucial habitats, and exposure to humans at

reserve edges. Development of a habitat quality and contrast measure, such as the one proposed here, may have the potential to capture cumulative habitat loss due to land use regardless of the driver (e.g. deforestation and land development) and to capture changes in habitat heterogeneity from that of the inside of PAs.

The value of surrounding areas as crucial habitats and population sources for species and ecological functioning in PAs is perhaps made even more essential by the non-random location of PAs relative to biophysical conditions. PAs are often located in relatively harsh biophysical settings and represent colder/hotter, drier, more topographically complex, and less productive portions of the broader ecosystem (Scott, Davis et al. 2001; Hansen and Rotella 2002). Thus, higher production and more suitable habitats outside these PAs may be vital as population, food and habitat sources for species of the region. For example, in many PAs, surrounding lands contain higher species abundance and richness, acting as population sources for PAs (Hansen and Rotella 2002). Moreover, in some cases PAs are delineated due to unique natural features or aesthetic values which may not coincide with a representative or ample sample of habitat features necessary to maintain ecological function or biodiversity.

The detrimental effects of land use expansion around PAs is then 3-fold as they may: 1) decrease the effective size of the PA and increases isolation; 2) functionally increase the biased location of natural habitats (Newmark 1987; Hansen and Rotella 2001); and, 3), reduce the viability of native species within nearby reserves. Maintaining PAs will require some level of conservation-oriented management in the unprotected portion of the ecosystem. Examining the current conditions PAs are situated within the surrounding landscape and how they may contrast with the landscape, will be a key for effective management.

NDVI as a measure of vegetation cover

Remote sensing provides the ideal tool for examining large area's of the earth's surface to analyze and monitor ecosystem patterns. To add to this, increasingly high-resolution passive-sensor imagery is fast becoming freely available with global coverage, lending itself to such applications and allowing novel approaches to be explored. Perhaps the features most easily identifiable with remote sensing, the physiognomy and spatial pattern of vegetation, are also among the most important since they characterize the landscape both structurally and functionally (Rocchini et al. 2006). The most widely applied and understood remotely-sensed spectral measure of vegetation growth and pattern is the normalized difference vegetation index (NDVI). The standard calculation of NDVI is: NIR – VIS / NIR + VIS (VIS = visible spectral measurement, NIR = near infrared spectral measurement). In theory NDVI measurements range between -1.0 and 1.0 however in practice the measurements generally range from -0.1 and +0.7. Clouds, water, snow and ice give negative NDVI values, while bare soils and other background materials produce values between -0.1 and +0.1. Larger NDVI values occur as the amount of green vegetation in the observed area increases.

Since NDVI correlates to the fraction of absorbed photosynthetic active radiation (FAPAR), it represents a practical proxy of the ecosystem NPP. The hypothesis that energy-related factors are the primary determinants of biodiversity is extensively supported (Gillespie et al. 2008). This relationship has been the basis for a bevy of studies, from arctic to tropical ecosystems, quantifying species richness, diversity and describing vegetation patterns using NDVI (Fairbanks & McGwire 2004; Lassau et al. 2005; Levin et al. 2007; Oindo & Skidmore 2002). NDVI has been used to explain between 30 and 87% of the variation in species richness or diversity within a vegetation type, landscape, or

region (Gillespie et al. 2008). While we do not make inferences about PA species richness at this stage from the contagion metric, this evidence illustrates the strong associations between NDVI and key ecosystem features (i.e. productivity and richness). DeFries' et al. (2005) Vegetation Continuous Fields (VCF) product, which they used to quantify forest cover extent and loss of forest habitat within and surrounding PAs, was in part derived from NDVI values.

High NDVI values are also strong predictors of habitat heterogeneity and are commonly used to characterize the landscape vegetation heterogeneity (LVH) at both regional and global scales (Gould 2000; Kerr et al. 2001). Contingent on the relationship between species richness and habitat diversity, wherein richness increases with LVH at a variety of scales (Heikkinen 1996; Macarthur 1965), a growing number of studies have applied spectral indices to estimate patterns of biodiversity (Gould 2000; Honnay et al. 2003; Palmer et al. 2002; Rocchini 2007). Most commonly, strong correlations between NDVI variance and field-based complexity scores have been employed to accurately estimate habitat heterogeneity, taxa richness, species distribution patterns, biodiversity hotspots, and even functional diversity along site gradients (Lassau & Hochuli 2008; Levin et al. 2007; Symonds & Johnson 2008; Zinner et al. 2001).

For example, Fairbanks and McGwire (2004) used a principle component analysis to reduce a five-year time series AVHRR dataset to three variables describing NDVI variability, and a fourth variable representing heterogeneity (computed from the standard deviation of the first NDVI variable). They tested these alternative variables as measures of floristic richness in vegetation communities of California (i.e., haparral, coastal sage scrub, and yellow pine forest). While the NDVI relationship with species richness varied across community types, richness was quite consistently and positively related to NDVI heterogeneity (r^2 values ranged from 0.26-0.81). Likewise, using a NDVI map

derived from a 30 m resolution Landsat Thematic Mapper image of a low-shrub tundra study site in the Canadian arctic, Gould (2000) showed a strong relationship between NDVI variability (standard deviation of NDVI values from 17 target areas of 500 pixels) and observed species richness. Gould showed that NDVI variability alone explained 65% of the variation in species richness, and noted that ground analysis from the most species-poor sites would increase the strength of this relationship.

The NDVI index is commonly used to characterize the landscape vegetation pattern at both regional and global scales (Gould 2000; Kerr et al. 2001). These studies suggest that maintenance of the landscape pattern of vegetation heterogeneity is correlated with the ecological integrity of a territory.

Contagion as a metric of landscape pattern

If we propose to use NDVI as a measure of vegetation cover, yet want to also measure vegetation structure and spatial pattern between PAs and their surroundings, we then need a measure of cover pattern to which we can apply NDVI. In the paper to follow we estimated the landscape pattern of vegetation heterogeneity by applying a standard landscape metric (i.e., contagion) to the spatiotemporal NDVI data of each PA and its corresponding buffers.

Contagion is an entropy-based metric extensively used to quantify the landscape homogeneity of patch types on raster categorical maps (O'Neill et al. 1988). The contagion metric has been adapted by Li and Reynolds (1993) and extended to measure the space–time dispersion of patch types. Space–time cubes full of large, contiguous, patch types give rise to high contagion (max = 1), whereas a completely random mix of small patch types gives low contagion values (min = 0). Contagion reaches its maximum when the landscape is

composed of just one patch type. Applying the contagion metric to spatiotemporal NDVI values has a number of advantages: 1) the metric is influenced both by the landcover composition (i.e., the relative dominance of greenness patch types) and configuration (i.e., the spatial arrangement of greenness patch types); 2) contagion provides a bounded measure of vegetation heterogeneity (homogeneity) at each pixel localization on the map; 3) when used on spatiotemporal data the metric may be interpreted as a measure of temporal stability, since a high seasonal variability in vegetation cover at a particular pixel localization should result in a lower contagion value. The time dimension can also help discriminate between landcover patterns with similar greenness values, but different seasonal dynamics (e.g., crops vs. forests).

LVH and variation in biodiversity are clearly important defining ecosystem properties, with strong relationships to vital ecosystem functions and population viability. The prominence of complexity measures in recent ecological literature even encourages a shift of emphasis from diversity (counts of biological objects at a given time and place) to complexity measures (spatiotemporal structure of a set of biological objects at a given scale) as Anand and Tucker (2003) originally proposed. Applying information theoretic indices, our contagion metric presents a novel method to capture spatiotemporal complexity (alternatively, uniformity) of NDVI values across a given landscape. Contagion not only incorporates vegetation intensity (greenness), but describes intrinsic spatial patterns of vegetation complexity at multiple scales of analysis, rather than simply computing NDVI variance for a given area. In addition, remotely-sensed measurements of habitat heterogeneity (NDVI contagion in this particular case) are dynamic and are capable of incorporating other factors that influence species distributions, such as disturbances (e.g. fire) and seasonal dynamics. As such, we suggest contagion captures key ecosystem patterns, comparable across ecosystems.

Contagion contrast as a metric of PA isolation

There are only two previous large-scale assessments that quantify landcover change in and around PAs. Both DeFries et al. (2005) and Joppa et al. (2008) use large worldwide samples of PAs (n = 198 and 1062 respectively) and explicitly quantify deforestation and habitat fragmentation in and around PAs. DeFries' et al. (2005) analysis was limited to moist and dry tropical forests and only high protection PAs (i.e., IUCN status I & II). Joppa et al. (2008) limited their analysis to moist tropical forests in four regions and included all IUCN protection levels. DeFries et al. (2005) explicitly address PA isolation, finding that nearly 70% of the PA buffers experienced habitat loss over the last 20 years. Joppa et al. (2008) measured forest cover inside and outside PAs and highlighted important geographical differences between PAs protected *de facto* (i.e., generally larger PAs retain forest cover inside and outside due to remote locations) vs regions where PAs are protected *de jure* (i.e., PAs generally retain forest cover because of their legal status, but PAs are small and their surroundings are highly fragmented). The mapping methods employed in these two studies were based on binary measures of tree cover (i.e., a measure of the percentage of forested land based on a 0 or 1 pixel value of forest cover) or categorized forest-type landcover products, and thus were limited to forest-dominated systems. Differing from the two previous studies, in the paper to follow, we focus on explicitly and empirically quantifying: how contrasted are PAs from their surroundings? To do so, we compare the contagion of spatiotemporal NDVI values from inside PAs to that of their surroundings using three buffers of increasing distance from the PA border (i.e., contagion contrast). Our method of applying contagion to the spatiotemporal NDVI data of PAs and their corresponding buffers (i.e., surrounding lands) can be applied, and is comparable, across a broader range of biomes and ecoregions. This contagion metric is independent of the vegetation cover type (i.e. patch type), and thus can

indicate whether the landscape pattern of vegetation heterogeneity inside PAs is representative of the surroundings independent of ecoregion types and socio-economic settings.

Objectifs de travail

The objective of this study is to explore the questions of: how isolated are PAs, as measured by their inside vs. outside difference in the landscape pattern of vegetation heterogeneity, and what are the common drivers of their isolation? We propose that PAs of low protection status, due to their less stringent resource use policies, should have landscape vegetation patterns more similar to their surroundings, and thus a lower degree of isolation. On the other hand, we propose that PAs embedded into a more altered landcover matrix, due to an intensification of human activities, should have landscape vegetation patterns more contrasted with their surroundings, thus a higher degree of isolation. Specifically, we predicted the degree of PA isolation to increase when: its protection status decreases (higher IUCN management category), the landcover alteration outside its border increases (higher human appropriation of net primary productivity), and when its geographical placement is biased to preserve biophysical features that may not be always representative of the larger region (higher elevation change between the PA and the surrounding landscape).

CHAPITRE I

A novel measure of protected area isolation: correlations with management, neighbouring landuse intensity and landscape features

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1.1 Abstract

There are now over 110 000 terrestrial protected areas worldwide, covering over 12% of the terrestrial surface of the Earth, and yet many are not maintaining ecological integrity as originally envisioned. Recent studies suggest that the fundamental reason protected areas are failing is an increasing contrast between the protected lands and the surrounding matrix of, often highly altered, landcover. This increasing contrast increases the isolation of the protected area, in that it increases the effective distance between the protected area and other protected or natural areas, since it becomes more and more difficult for wildlife to traverse the increasingly hostile matrix. To quantify protected area isolation we used the contagion metric of NDVI values, which include the seasonal dynamics of monthly NDVI data, and compared the pattern of landcover vegetation heterogeneity inside protected areas to the pattern outside their borders. Contagion was computed for a sample of 114 protected areas distributed worldwide and for three buffers at increasing distances from their borders. Our analysis showed that the isolation of protected areas is significantly positive in 110 of the 114 areas, indicating that the landcover heterogeneity is consistently higher (i.e., more fragmented) 10-20 km outside a protected area than inside its borders. Unlike previous studies, we found an effect of the IUCN protection status on protected area isolation. Isolation was significantly higher in areas with high protection status compared to those with low protection status. High-protection areas show higher isolation, probably due to the effectiveness of their management strategies at preserving the integrity of the landcover pattern within the protected areas relative to the neighboring unprotected lands. However, while the intensification of human activities in lands surrounding low-protection areas explains a significant proportion of the variance in their isolation, the same is not true for high-protection areas. This could be due to their more remote geographic placement than low-protection areas. The inside–outside contagion metric provides a novel way to assess the isolation of protected areas embedded in different environmental, social, and economic contexts.

Keywords: parks, reserves, landcover heterogeneity, fragmentation, landscape matrix, complexity, HANPP, IUCN

1.2 Introduction

The World Conservation Union definition of a protected area is a piece Earth regulated for preserving ecological integrity (UNEP 2009). Ecological integrity in this context is the ability of an ecosystem to maintain species composition, diversity, and functional organization comparable to those of areas with little human activity or impact. The last three decades have seen the global coverage of nationally protected areas triple from nearly 6x106 km2 in 1980, to nearly 18x106 km2 in 2009, yet many protected areas are not maintaining their ecological integrity (Hansen & DeFries 2007). Despite that protected areas generally achieve their basic management goals and effectively enforce their policies (e.g., prevent land clearing, mitigate logging and hunting) (Bruner et al. 2001), extirpations and extinctions continue to occur inside their borders (DeFries et al. 2005).

A growing body of research acknowledges that the fundamental reason protected areas are failing is an increasing discontinuity in the spatial pattern of vegetation heterogeneity between the protected lands and the surrounding matrix of, often highly altered, landcover (Parks & Harcourt 2002; DeFries et al. 2005; Hansen & DeFries 2007; Newmark 2008). Using the Vegetation Continuous Fields product as a measure of forest cover loss, DeFries' et al. (2005) reported that nearly 70% of the buffers surrounding protected areas in moist and dry tropical forests (IUCN management category I & II) have experienced landcover alteration over the last 20 years. High human population density, loss of natural landcover, and small reserve size have all been equated to forms of protected area isolation (Newmark 1995; Bruner et al. 2001; Peres 2005; DeFries et al. 2007) and negative correlations between species extinctions and these forms of isolation have been documented (Parks & Harcourt 2002; Newmark 2008). Thus, the effectiveness of protected areas depends on processes operating

both outside and inside their borders; e.g., animal migration and distribution, geochemical cycling, or natural disturbances that may not restrict to the delineation of protected area borders.

Empirical and theoretical analyses suggest that protected area isolation can arise from either a biased placement away from landcovers that are representative of the greater region, towards more extreme geographic settings (e.g., cold, dry, high altitude, low productivity habitats) (Scott et al. 2001; Hansen & Rotella 2002; Hansen & DeFries 2007), or from intensifying landcover alteration outside protected area borders (DeFries et al. 2005; Hansen & DeFries 2007; Joppa et al. 2008; Newmark 2008). Though the integrity of the landcover matrix surrounding protected areas is crucial to maintaining conservation priorities (Franklin & Lindenmayer 2009), there are no standardized methods that compare the isolation of areas embedded in different environmental, social, and economic contexts.

Here we quantify protected area isolation by comparing patterns of landcover vegetation heterogeneity inside and outside their borders. Isolation is calculated from the contagion metric of NDVI values (Normalized Difference Vegetation Index) within each area and a series of surrounding buffers. NDVI values have been used to measure productivity and characterize the vegetation cover at both regional and global scales (Gould 2000; Kerr et al. 2001), and contagion is an extensively used metric quantifying the heterogeneity of landcover categories across a landscape (Li & Reynolds 1993). Previous studies using NDVI maps suggest that loss of ecological integrity, as measured by a decrease in biomass productivity or species richness of an area, is correlated to changes in landcover heterogeneity (Gould 2000; Honnay et al. 2003; Barbosa et al. 2006; Ding et al. 2006; Levin et al. 2007; Rocchini 2007; Gillespie et al. 2008; Kumar et al. 2009). Therefore, the pattern of vegetation heterogeneity of a

protected area should be a useful indicator of its ecological integrity and, subsequently, a useful measure of the contrast (i.e., isolation) between an area and the surrounding landscape matrix.

The objectives of this study are to: explore the extent to which protected areas of the world are isolated, as measured by the difference in patterns of vegetation heterogeneity inside and outside their borders; and to relate this novel measure of isolation with factors of landcover alteration, protection status, and the geographical placement of protected areas.

1.3 Methods

1.3.1 Sample of protected areas

The World Database on Protected Areas (WDPA) (UNEP 2009) is the most complete data set on the global distribution of protected areas. We selected 114 protected areas from this database on the basis of the following five criteria. First, we selected protected areas within a size range of 50 000 to 70 000 ha. Protected areas of this size are large enough to potentially include several vegetation cover types, but not overly large as to cross ecoregion boundaries. It furthermore represents the modal range in the log-normalized size frequency distribution of all terrestrial protected areas in the WDPA database. Thus, this size range represents the protected areas most common worldwide. Second, we selected only terrestrial protected areas having an IUCN management category between I and V, where protection status decreases with increasing IUCN management category. Category VI areas were excluded because they allow continual resource extraction within their borders (see IUCN management category definitions), which we assume results in landcover alterations that would render them indistinguishable from their surrounding lands using our

measure (i.e., no detectable isolation effects). Third, we eliminated protected areas whose 10-20 km buffers largely overlapped coastlines or large water bodies. We did not want factors unrelated to vegetation cover (such as large areas of surface water) to affect the pattern of landcover heterogeneity outside protected area borders. Fourth, we removed protected areas that were part of reserve networks or shared borders with other protected areas (i.e., protected areas that had other protected areas within 20 km of their border). Here we did not want other protected areas influencing the landcover of the unprotected lands in the outside buffers. Fifth, we screened the remaining protected areas to ensure a balanced representation of biomes and continents across the globe. Our final sample of protected areas represented 18% of all protected areas in the selected size range (Fig. 1; S1 of Appendix).

1.3.2 Spatiotemporal NDVI values

We derived 32-day composite NDVI maps, for each month of 2005, from the Moderate Resolution Imaging Spectroradiometer (Modis, 500 m resolution) red and near-infrared composite bands (NASA 2007). Values of NDVI are calculated as: NIR – RED/NIR + RED (NIR = near-infrared and RED = red, spectral reflectance) (Tucker 1979). We created three non-overlapping outside buffers of 0-5 km, 5-10 km and 10-20 km from each protected area's border using the buffer wizard in ArcInfo (ESRI 2009). A 10-20 km buffer around protected areas was deemed large enough to identify substantial changes in landcover and still be within a wider zone where ecological mechanisms and natural disturbances influence the species and ecosystem processes within the protected area (Hansen & Defries 2007). We transformed the polygons and buffers of the protected areas into rasters with the polygon-to-raster function (ArcInfo) and projected them on the Modis NDVI maps. All geographic coordinates of pixels

and associated NDVI values were then exported to Matlab (Matlab 2009) for subsequent analyses.

1.3.3 Measuring isolation of protected areas

For each protected area and its three buffers we calculated the contagion value for a window centered on each 500x500m NDVI pixel and then averaged across windows to give a mean contagion value for the whole area. The mean contagion inside the protected area was then subtracted from the mean contagion of three non-overlapping buffers, at 5, 10 and 20 km from the protected area border. This produced, for each protected area, three measures of isolation at increasing distances. Protected area isolation is positive when the mean contagion inside the protected area is higher (more uniform) than outside its border, or negative when the mean contagion inside the protected area is lower (more heterogenous or fragmented) than outside. Since protected areas of greater protection status, surrounded by a comparatively more altered landcover, should increase their degree of isolation, we considered negative inside-outside differences in mean contagion as indicative of a lower degree of isolation.

We quantified the pattern of landcover vegetation heterogeneity by calculating the contagion of NDVI values (O'Neill et al. 1988; Li & Reynolds 1993). We first linearly rescaled all the NDVI values into 15 landcover (vegetation cover) categories. Using existing Matlab codes (see Parrott et al. 2008), we adapted the contagion metric to measure the space–time heterogeneity of these landcover categories. By incorporating a temporal component to the contagion metric with the inclusion of monthly NDVI values, protected area isolation could be measured not only by inside-outside differences in the spatial pattern of vegetation heterogeneity, but also by inside-outside differences in

seasonal dynamics. For example, protected area isolation would increase in cases where the vegetation cover inside and outside protected areas share similar greenness levels and landcover patterns, yet different seasonal dynamics (e.g., a protected area dominated by a natural landcover of evergreen forest embedded in a region dominated by intensive agriculture). Contagion is high (max = 1) if the landcover heterogeneity is composed of just one or two categories of vegetation cover intensity, whereas contagion is low (min = 0) when the landcover is randomly distributed and covers the full range of vegetation cover categories.

To explore the effect of window size, we modified the spatial neighborhood of the contagion metric by using four window extents centered on each pixel of the NDVI map (3, 5, 7, and 9 pixels; corresponding to 1.5, 2.5, 3.5. and 4.5 km2). We found that the inside-outside differences in mean contagion values (i.e., isolation) calculated on the basis of the four window extents were highly correlated across protected areas (all Pearson's r above 0.95). We therefore retained the 3.5 km window and used only protected area isolation values from this extent in statistical analyses. Finally, we compared the protected area isolation values obtained with the 12-month NDVI series to those obtained from only the 6-month period of May to October 2005. We did this to examine whether selecting only peak months of greeeness, vs an entire year, had an effect on contagion values since the globally distributed data covered several biomes.

1.3.4 Statistical analyses and predictors of isolation

Given the large sample size (number of pixels) inside and outside PAs we used a bootstrap procedure to account for the uncertainty associated with our measure of protected area isolation. We re-sampled a subset of contagion values inside and outside protected areas without replacement (Molinaro et al. 2005) to

account for the irregular (often multi-modal) distribution of contagion values across the landscape. With this procedure the mean contagion inside and outside was obtained from equal sample sizes and independent bootstrap samples (i.e., repeated samples do not share pixels), ensuring that the confidence intervals do not generate inflated Type I error rates. For each protected area and buffer zone, we repeated the bootstrap procedure 1 000 times for a subset of 100 pixels inside and outside protected areas. We recorded the mean contagion difference and 95% confidence intervals (CI) as a measure of protected area isolation. The isolation of an area was considered significant if the 95% confidence intervals of the inside-outside differences in mean contagion excluded zero and if the effect size (i.e., the protected area isolation value) was greater than ±0.05.

We considered four potential predictors of isolation as measured by our metric. First, elevation change, as an indicator of isolation caused by the geographic placement of protected areas in high altitude or topographically complex lands. The mean elevation inside protected areas and the three surrounding buffers was extracted from the Shuttle Radar Topography Mission (SRTM) 90m Digital Elevation model (Jarvis et al. 2008). Elevation change was calculated as the mean inside protected area elevation minus the mean outside elevation (calculated using a 20 km buffer). Second, the percentage of human appropriation of net primary productivity (% HANPP) was used as a generic measure of landcover alteration. Values of human appropriation of net primary productivity estimate the relative percentage of carbon required to derive food and fiber products consumed by humans on a per capita basis, applied to globally distributed population data (Imhoff et al. 2004). We attributed to each protected area the % HANPP value from the one-quarter degree resolution grid-cell nearest to the coordinate for the protected area. Third, IUCN protection status as a measure of management intensity inside protected areas. We grouped protected areas into high-protection (IUCN category I-III) and low-protection

(IUCN category IV-V) categories. Fourth, the globally-ranked conservation status of the protected area's ecoregion (Olson & Dinerstein 2002). Here, protected areas were grouped according to the conservation status of the ecoregion in which they are located. Protected areas in stable and vulnerable ecoregions were categorized as non-endangered, while protected areas in endangered ecoregions were categorized as endangered.

Potential predictors of isolation, like % HANPP and the IUCN protection status, should be representative of the global reserve network and independent of the biome or continent where protected areas are located. In technical terms, this condition imposes that the residuals of our regression models are not spatially auto-correlated. Furthermore, according to our proposed measure, isolation values for protected areas may be high regardless of whether mean NDVI (greenness) is high or low. Nevertheless, a high isolation value may be more detrimental to the ecological integrity of areas located in lowland rainforest areas (i.e., low variation in NDVI values and high greenness overall) than it is to areas located in hot or cold deserts (i.e., higher NDVI variation and lower greenness). To account for global-scale differences among protected areas we calculated the coefficient of variation (CV) in greenness (NDVI) values inside each area. The reciprocal of the CV NDVI is known as the signal-to-noise ratio, which here quantifies the average greenness of an area (i.e., the mean of NDVI values) scaled to the variation in its vegetation cover (i.e., the standard deviation of NDVI values). The inclusion of the CV NDVI variable was also expected to prevent spatial auto-correlation of residuals in our regression models.

Including the above five predictors (i.e., elevation change, % HANPP, IUCN protection status, ecoregion conservation status, and CV NDVI), we fitted a regression model to the isolation values of our 114 PAs. For protection status we used a dummy variable representing the contrast between high-protection

(IUCN category I-III) and low-protection status (IUCN category IV-V). For ecoregion conservation status we used a dummy variable representing the contrast between protected areas located within endangered ecoregions (endangered) and protected areas not located within endangered ecoregions (non-endangered category). We fitted a separate regression model for each of the three buffers. We based model selection on all-subsets following Sheather (2009), using the adjusted coefficient of determination (R2). We note that selection based on Bayesian information criterion selected exactly the same models. To assess whether spatial autocorrelation in model residuals could bias statistical testing or indicate potential missing variables (Peres-Neto & Legendre 2010), we calculated global Moran's autocorrelation coefficient I for model residuals (see Table 1) and correlograms testing for autocorrelation in residuals at different scales (not shown here). We log transformed all non-categorical predictor variables to improve multi-normality and stabilize variances. Normal probability plots (Q-Q plot) indicated that model residuals were nearly normal.

1.4 Results

Protected area isolation for both the 0-5 km and 5-10 km buffers varied across the sample (Table 1; all contagion values and variable results for each PA are presented in this table), and included significantly positive, significantly negative, and non-significant values; the latter occurred in more than three-quarters of the protected areas at the 0-5 km and 5-10 km buffer distances. In contrast, the protected area isolation values for the 10-20 km buffer were significant in 110 of 114 areas and was consistently positive and high, meaning that landcover in the 10-20 km buffers was more heterogeneous and more fragmented (contagion was lower) than inside the protected areas. Also, isolation measured as the difference between mean contagion in the 10-20 km buffer vs.

inside the protected area was always higher than when it was measured using the difference between mean contagion in the 0-5 km or 5-10 km buffers vs. in the protected area. In summary, the contrast between the landcover pattern (contagion) in the protected area vs. in the surrounding area (protected area isolation) increased with distance from the border of the protected area (Appendix S1; Fig. 2).

We found highly positive correlations between protected area isolation values obtained for adjacent buffers (isolation 10-20 km vs. 5-10 km, $r2 = 0.69$, $p < 0.001$; isolation 5-10 km vs. 0-5 km, $r2 = 0.89$, $p < 0.001$). For example, PAs with a high degree of isolation 0-5 km away from their borders also showed a high degree of isolation at 10-20 km. Moreover, we found a strong positive correlation between isolation values calculated from the 12 months of 2005 and from only the 6 months from May to October ($r2 = 0.98$, $p < 0.001$).

Protected areas with a lower CV NDVI ratio (uniformly greener) inside the reserve tended to have higher isolation values (Fig. 2). Both the % HANPP and the IUCN protection status predictors had a positive effect on protected area isolation for the 5-10 km and 10-20 km buffers (Table 2; Fig. 3). Protected area isolation was significantly higher in areas of high protection status (IUCN categories I-III; Fig. 3). The total amount of explained variation (R2) by the different models increased as the distance of the buffer from the protected area increased (Table 2). The global Moran's autocorrelation coefficient (Table 2) and correlograms testing for autocorrelation in the residuals at different scales (not shown here) did not show spatial autocorrelation in residuals for any of the three models produced. The lack of spatial trends in model residuals indicates that the relationships we detected do not differ in different parts of the globe, thus strengthening the generality of our results.

Elevation change did not have a significant relationship with protected area isolation and it was not retained in any of the final models (Table 2). However, we do note that high-protection areas are generally established in regions of higher elevation than are low-protection areas (high-protection areas max. altitude (± 1SE): 1648m (180), low-protection areas max. altitude (± 1SE): 1134m (134), $t = 2.286$, $p = 0.0223$), so the effect of elevation change may be masked by the relationship between isolation and protection status.

The ecoregion conservation status of protected areas did not enter any of the final regression models either. However, when protected areas were grouped by the conservation status of their ecoregion (endangered or non-endangered), isolation increased with increasing % HANPP for protected areas in ecoregions of endangered status (Fig. 4). A chi-square test determined that there was no significant association between the IUCN protection status of areas and the conservation status of their ecoregion ($\chi 2 = 2.591$, $p = 0.1074$), eliminating the possibility of confounding the two effects.

1.5 Discussion

The vast majority of protected area isolation values were significant and positive for the 10-20 km buffer. That is to say, at a distance 10 km from their border, most protected areas in our sample had a measurable level of isolation because the surrounding landcover was significantly more fragmented and heterogenous than that of the protected area. Isolation, measured by contagion, always increased as the distance from the protected area border increased. Furthermore, protected area isolation values increased sharply at the 10-20 km buffer distance relative to the 5-10 km and 0-5 km buffers. These findings suggest that human alteration of vegetation heterogeneity is less intense within

10 km of protected areas, and increases abruptly at 10-20km from the protected area border. Considering that human appropriation of primary productivity in unprotected lands is intensifying (Hansen & DeFries 2007), this form of isolation is likely to rise.

Our contagion metric based on NDVI maps expands on the previous studies quantifying protected area isolation (DeFries et al. 2005; Joppa et al. 2008). Previous studies developed isolation metrics based on a binary [1, 0] classification of tree cover; such metrics are only applicable to forest-dominated ecosystems. In contrast, our metric is comparable across different ecosystem types. In fact, our metric sometimes produced different isolation values than metrics based on tree cover classifications. For example, the protected area Serra do Itaja (Brazil) is ranked in the lowest category of deforestation rates in DeFries' et al. (2005) analysis based on extent of natural forest loss within and surrounding the protected area. However, this protected area has the highest isolation value in our dataset when contagion inside is compared to contagion in the 10-20 km buffer. Earlier metrics of protected-area isolation, as in the example above, may not have captured discontinuity in landcover heterogenetiy as distance from the border increased because only the percentage of tree cover was measured and not differences in spatial or seasonal vegetation patterns.

We did not examine protected areas that were surrounded by other reserves. This selection criterion may bias our sample towards isolated PAs. Joppa et al. (2008) pointed out that in the African Congo and Amazon Basin, protected areas were established in remote regions surrounded by protected forests and thus showed little difference in forest cover outside their borders. In regions where protected areas are not surrounded by other reserves, their results are in congruence with ours and those of DeFries et al. (2005); leading to the conclusion that the vegetation pattern of an overwhelming majority of protected

areas is becoming increasingly different from that of the surrounding landcover matrix, and thus isolating them from other natural areas with similar landcover patterns.

All variables but elevation change explained significant variance in protected area isolation when considering one or many buffer distances. However, our best statistical model explained only 24% of the overall variance in protected area isolation. Still, a large part of that variance was explained by one variable (CV NDVI). The negative relationship of CV NDVI with isolation indicates that different regions of the world have different predispositions to isolation. Lowland regions covered by evergreen forests (i.e., lower CV NDVI) may have a higher propensity towards high degrees of isolation. This is illustrated from the fact that, among protected areas showing the highest isolation at 10-20km, four of the first five areas are located in tropical forests (Appendix S1). Moreover, a high isolation value may be more detrimental to the ecological integrity of protected areas with a uniformly green landcover (at least in terms of gross primary productivity losses and local species extinctions) than to areas with a more heterogeneous and less green landcover, as in drier regions of the world. Therefore, before considering any other anthropogenic factors of isolation, protected areas often considered of primary conservation value (e.g., tropical forest) may also be the most susceptible to isolation.

What are the factors responsible for the 76% of variation in protected area isolation that remains unexplained? With further application of the proposed metric, perhaps additional regional, economic, and cultural drivers of protected area isolation can be identified. These drivers are likely to be local variations in water and geological features and land uses, such as agriculture, forestry and urbanization. Incorporation of landuse categorical maps will help identify the landscape processes that generate protected area isolation, particularly in highly

protected areas. However, a more detailed understanding of the environmental and socio-economic processes underlying protected area isolation may come at the expense of models that are not so easily generalized to the global reserve network.

The premise of the IUCN categories is that conservation objectives are most likely to be achieved in protected areas with the most stringent resource use and conservation management policies (i.e., categories I-III). However, Joppa et al. (2008) concluded that relative forest cover in and around protected areas varies little among IUCN categories. The authors did note that their analysis may simply have been too coarse to pick up on the differences related to management categories (Joppa et al. 2008). Our results were more consistent with the expectations that the IUCN categories would dictate, since we found that high-protection areas were more effective at maintaining the ecological integrity of their interior (i.e., more uniform and less fragmented landcover than low-protection areas) Subsequently, protected area isolation was higher in areas with higher levels of protection (IUCN categories I-III) than in areas with lower levels of protection (IUCN categories IV and V).

We caution, however, that the increased isolation of high-protection areas could be due to the fact that high-protection areas generally occur at higher altitudes. If high-protection areas are located in lands with higher elevations, higher/lower temperatures, lower productivity, and/or more complex topography than their surroundings, these features may produce landcover patterns (e.g., vegetation heterogeneity or seasonal patterns) that are measured by the NDVI based contagion metric as isolation. However, elevation change, as calculated here over the larger region (including both the protected area itself and its surrounding buffers) was not associated with protected area isolation. Nevertheless, the potential negative effects of protected area isolation on species

and ecological integrity, due to an intensification of human activities in the neighboring lands, may happen much more rapidly in areas that are already naturally isolated.

A measure of human-induced landcover alteration surrounding protected areas (% HANPP) was significantly and positively related to our isolation metric, mainly in low-protection areas. This relationship was significant despite the landcover pattern inside low-protection areas being more fragmented than that of high-protection areas. However, this result does not necessarily suggest an absence of landcover alteration due to human activities outside high-protection areas.

A prominent issue in recent research has been whether protected area establishment encourages human settlement and population growth or whether protection deters settlement and land alteration beyond their borders (Wittemyer et al. 2008; Joppa et al. 2009). Isolation may be a diffusive process, where anthropogenic processes altering landcover invade towards the protected area through time, while internal influences (i.e., management policies which limit resource use and landcover alteration) appear also to extend beyond borders and into the nearby unprotected lands (0 -10 km from the border). This point is indirectly supported by two of our results. First, we found strong correlations among the protected area isolation values calculated from the three non-overlapping buffer zones; and second, we found that the largest inside-outside difference in mean contagion was always observed for the farthest buffer (10-20 km from the border). Likewise, Joppa et al. (2009) argued that population growth near the borders resulted from a general expansion of nearby human population settlements. These findings could also explain why the relationship between % HANPP and protected area isolation is stronger among low-protection

areas, which are typically placed closer to centers of dense human activities (Hansen & Rotella 2002).

At the present, we cannot infer the level isolation that would impact species persistence and ecological integrity. However, we can make qualitative linkages between our metric and these conservation objectives. Lindenmayer et al. (2009) recently emphasized the importance of preserving structural characteristics of the landcover matrix (e.g., retaining patches of preexisting forest types in a plantation landscape) for the maintenance of vertebrate populations. The positive relationship between protected area isolation and % HANPP we observed for protected areas in endangered ecoregions indicates that the conservation status of a protected area is linked to its degree of isolation and the level of anthropogenic land alteration in nearby unprotected lands. As the conservation status of an ecoregion depends largely on the number of threatened species in the region and the majority of an ecoregion's taxa are likely to be found in its protected areas, this relationship suggests that high isolation may translate into a net loss of ecological integrity.

Calculating the inside-outside differences in mean contagion from spatiotemporal NDVI maps represents a novel method to compare the isolation of protected areas embedded in different environmental, social, and economic contexts. Our analyses suggest that a majority of protected areas may be compromised in some way. If we consider landcover isolation a significant threat to protected area efficacy in limiting species extirpations and maintaining ecological integrity, our results raise an alarming aspect, perhaps representative, of the global protected area network. Areas that we deem most valuable and capable of maintaining ecosystem functions, high-protection areas, are those which are the most highly contrasted with their surroundings. This is probably due to the effectiveness of management strategies at preserving the integrity of

the landcover vegetation patterns inside high-protection area borders. Highly protected areas are also often established in unusual or remote regions, perhaps making them more prone to future isolation due to an intensification of human activities outside their borders. Low-protection areas showed lower isolation values likely because they are less successful in preserving the pattern of landcover vegetation heterogeneity inside their borders, although their degree of isolation appears more directly affected by human activities in the surrounding lands.

A bevy of studies, from arctic to tropical systems, have directly related patterns of landcover vegetation heterogeneity to plant species richness and diversity (Ding et al. 2006; Levin et al. 2007; Gillespie et al. 2008). Remotely sensed physiognomy and spatial pattern of vegetation are also important features because they characterize the landscape both structurally and functionally (Rocchini 2007). As such, NDVI values are commonly used to characterize the landscape vegetation heterogeneity at both regional and global scales (Gould 2000; Kerr et al. 2001), which in turn has served to estimate faunal species richness and distribution (Lassau & Hochuli 2008; Symonds & Johnson 2008; Kumar et al. 2009). These studies provide further justification for our application of NDVI maps to identify protected area isolation through differences in vegetation heterogeneity between protected areas and their surroundings.

1.6 Acknowledgements

Financial support to I. Seiferling was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC) for this work. We thank Melanie Desrochers for her technical support, contributions and valuable comments.

Figures:

Fig. 1: Longitude and latitude coordinates of the 114 protected areas overlaid on the SRTM world digital elevation model.

Fig. 2: Relationships between protected area isolation values, measured as the difference between mean contagion inside and in three non-overlapping buffers outside each area, and the coefficient of variation in greenness values (CV NDVI).

Fig. 3: Relationship between protected area isolation (inside-outside differences in mean contagion) and the % HANPP index, for buffer zones at A) 10-20 km and B) 5-10 km from the border. Areas are grouped by their IUCN management (protection) status. The lines indicate significant relationships obtained from bivariate linear regression models. Relationship between % HANPP and protected area isolation at A) 10-20 km (low-protection status: $n = 60$, $r2 = 0.11$; $p = 0.011$) and at B) 5-10 km (low-protection status: $r2 = 0.07$; $p = 0.04$).

Fig. 4: Relationship between protected area isolation (inside-outside differences in mean contagion) and % HANPP, for buffer zones at A) 10-20 km and B) 5-10 km from the border. Areas are grouped by the globally-ranked conservation status of their ecoregion (Olson & Dinerstein 2002). The lines indicate significant relationships obtained from bivariate linear regression models. Relationship between % HANPP and protected area isolation at A) 10-20 km and % HANPP (endangered status: $n = 68$, $r2 = 0.06$; $p = 0.041$) and at B) 5-10 km (endangered status: $r2 = 0.15$; $p = 0.0012$).

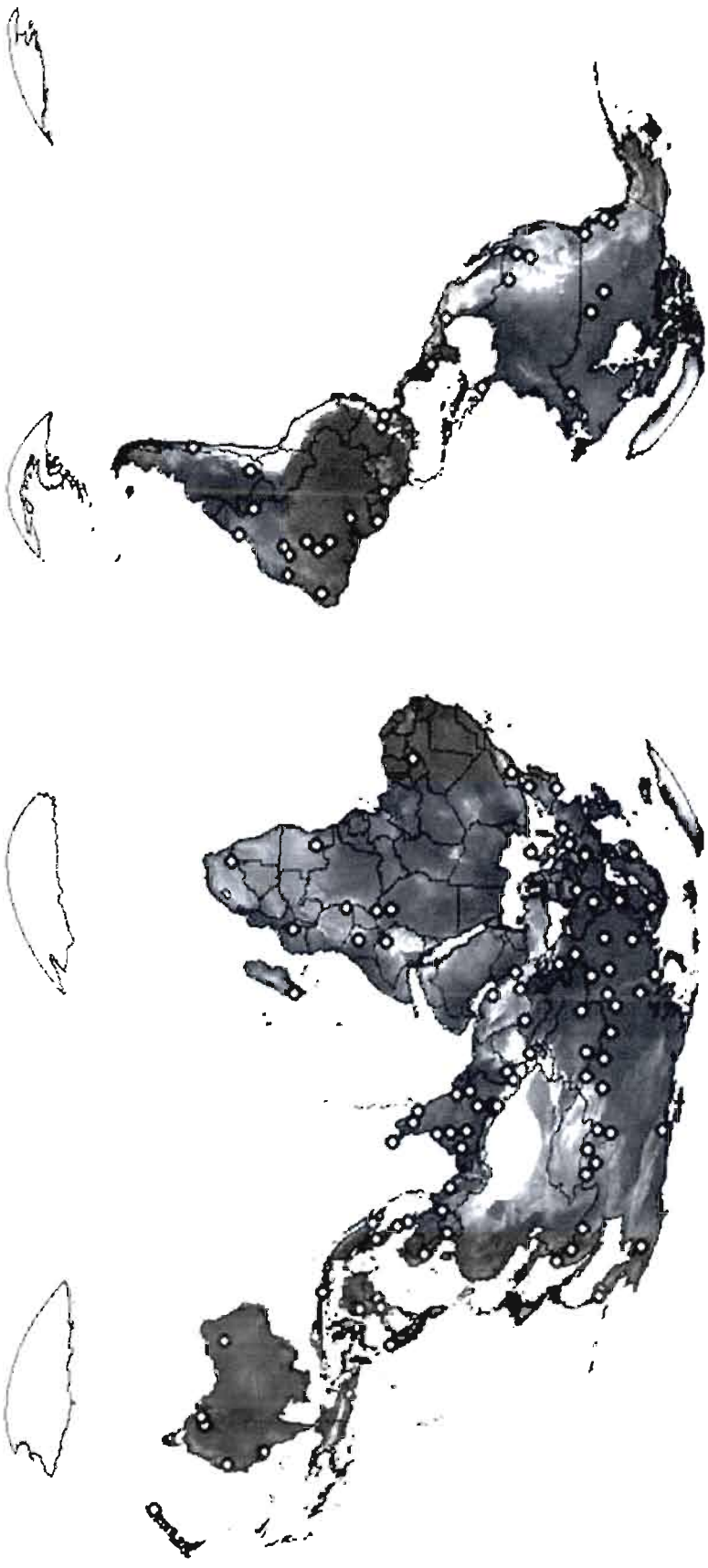

Figure 1

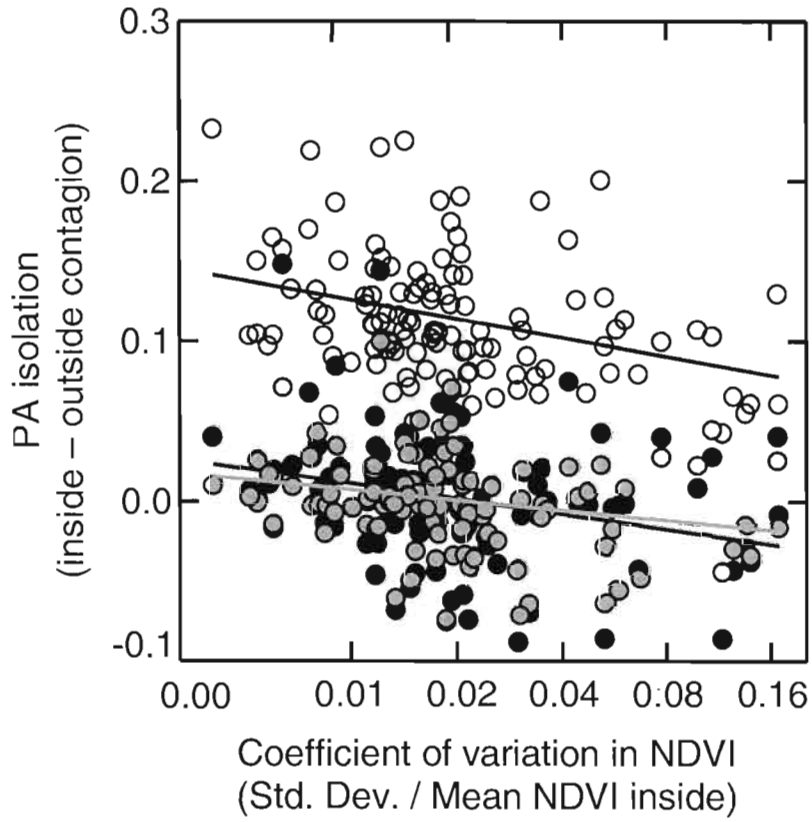
0.3
0.2
0.1
0.0
-0.1
PA isolation
(inside – outside contagion)
0.00
0.01
0.02
0.04
0.08
0.16
Coefficient of variation in NDVI
(Std. Dev. / Mean NDVI inside)

Figure 2

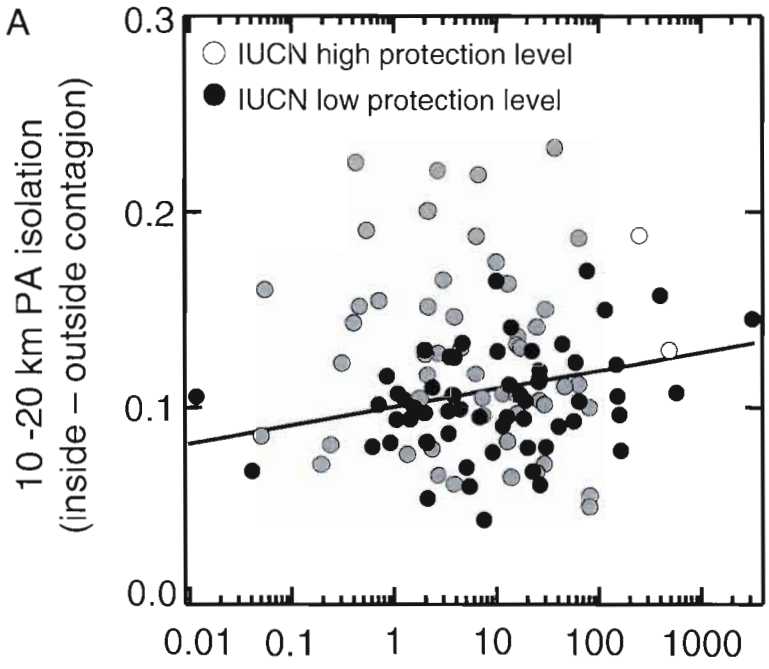
A
10 -20 km PA isolation
(inside – outside contagion)
0.3
0.2
0.1
0.0
IUCN high protection level
IUCN low protection level
0.01
0.1
1
10
100
1000

Figure 3-A

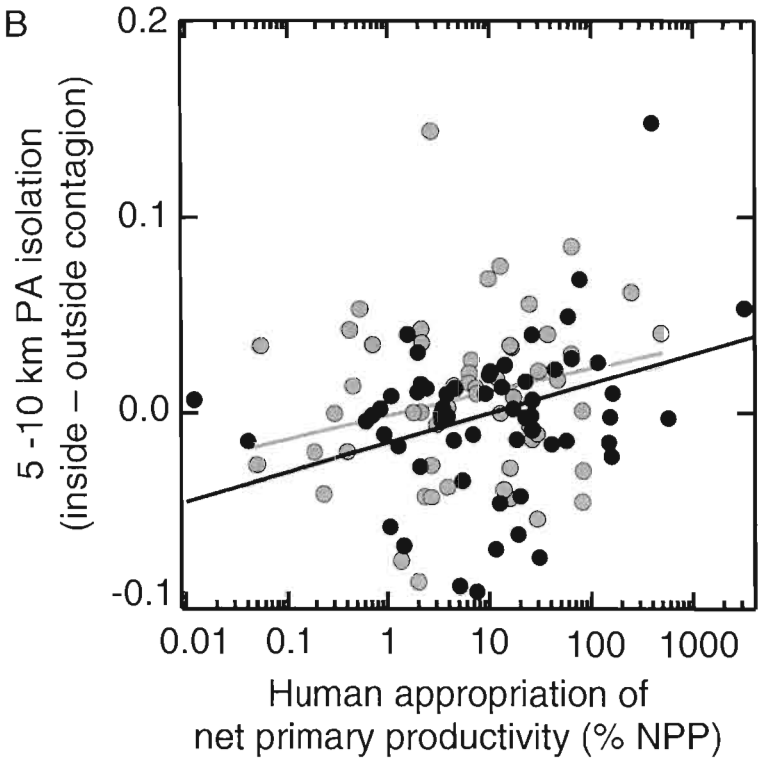
B
0.2
0.1
0.0
-0.1
5 -10 km PA isolation
(inside – outside contagion)
0.01
0.1
1
10
100
1000
Human appropriation of
net primary productivity (% NPP)

Figure 3-B

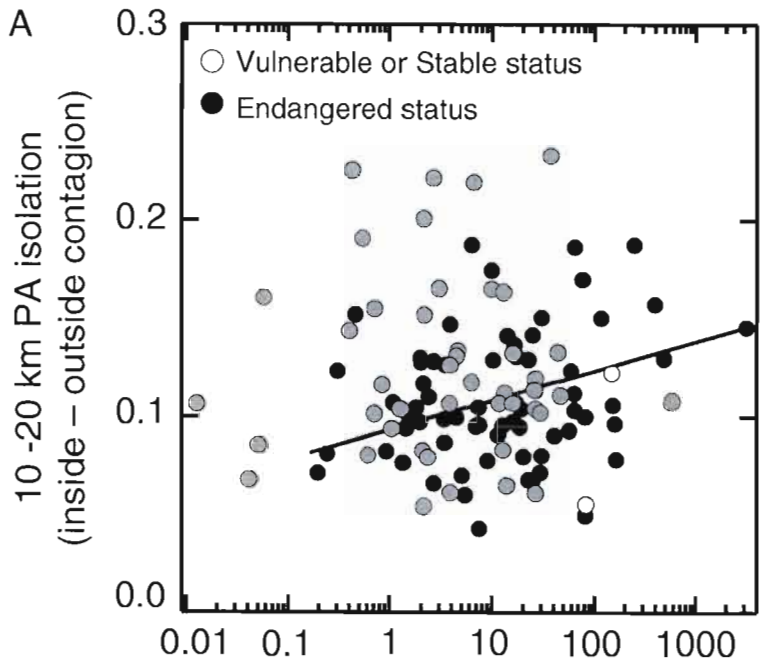
A
0.3
0.2
0.1
0.0
10 -20 km PA isolation
(inside – outside contagion)
Vulnerable or Stable status
Endangered status
0.01
0.1
1
10
100
1000

Figure 4-A

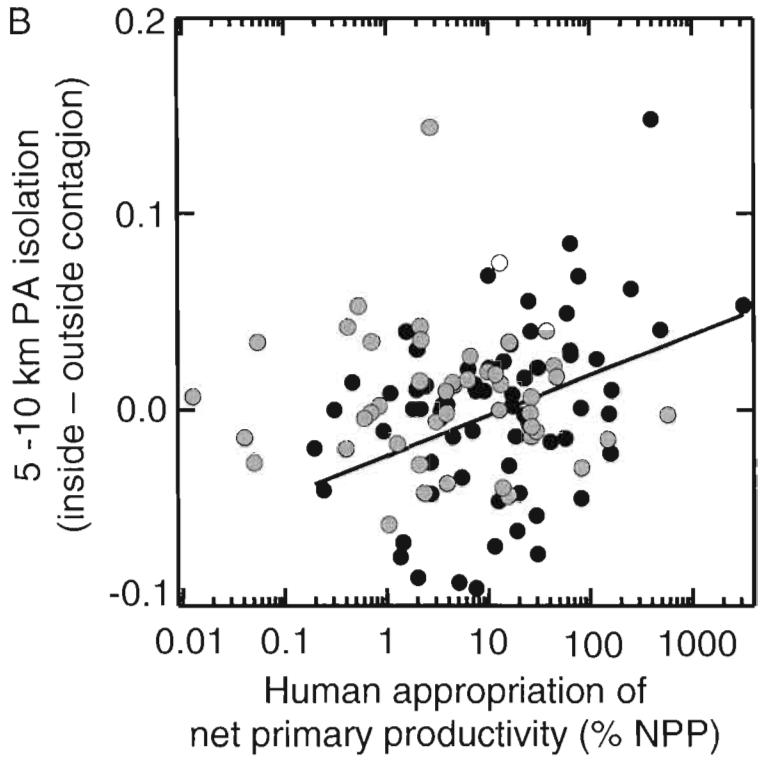
B
0.2
0.1
0.0
-0.1
5 -10 km PA isolation
(inside – outside contagion)
0.01
0.1
1
10
100
1000
Human appropriation of
net primary productivity (% NPP)

Figure 4-B

Tables

Table 1. Complete dataset of the 114 protected areas (PA), including predictor and response variables used in statistical models and figures. PA isolation values in bold are areas which 95% confidence interval (C.I.) excludes zero.

Protected Area	Country	Longitude	Latitude	Altitude min (m)	Altitude max (m)	IUCN Category (I-V)	Net Primary Productivity (g C m^{-2} y^{-1})	Human percent appropriation of NPP (%)	Global Conservation Ecosystem Status (Nature Serve G-Rank)	Mean NDVI Inside (0-1)	Std. NDVI Inside
Serra do Itajaí	Brazil	-49,1848	-27,1082	150	903	II	1166	37,9339	Vulnerable	0,9296	0,0036
El Rey	Argentina	-64,6202	-24,6914	793	2146	II	922	0,4346	Vulnerable	0,9053	0,0127
Reserve del Bosque Mbaracayú	Paraguay	-55,4060	-24,1351	152	461	II	1281	2,7096	Vulnerable	0,9309	0,0111
Pico Bonito	Honduras	-86,8724	15,6099	26	2278	II	1232	6,7369	Vulnerable	0,9222	0,0069
Mount Kenya	Kenya	37,3355	-0,1142	2393	4774	II	574	2,1694	Stable	0,7755	0,0402
Eungella	Australia	148,5660	-21,0046	92	1151	II	1359	0,5477	Vulnerable	0,8937	0,0182
Bromo Tengger Semeru	Indonesia	112,9391	-8,0322	825	3426	II	578	252,8746	Endengered	0,8967	0,0159
White Sands	United States	-106,3277	32,7815	1182	1269	III	84	6,4197	Endengered	0,6027	0,0209
Khao Luang	Thailand	99,7143	8,5409	73	1648	II	857	65,2881	Endengered	0,8838	0,0078
Zion	United States	-113,0316	37,2971	1128	2566	II	151	10,1047	Endengered	0,6945	0,0133
Sadej Naikom	Thailand	99,1722	11,0124	78	769	IV	104	78,0355	Endengered	0,8857	0,0066
Augrabies Falls	South Africa	20,1735	-28,5372	439	844	II	132	3,0734	Vulnerable	0,6131	0,0122
Pu Huong	Viet Nam	104,8644	19,3651	240	1405	IV	974	10,0275	Stable	0,9032	0,0053
Nanda Devi	India	79,8804	30,4051	2226	7280	I	121	13,1668	Vulnerable	0,5393	0,0226
Swan Lake Kispiox River	Canada	-128,6648	55,8019	416	1055	II	565	0,0558	Vulnerable	0,8392	0,0097
Jajrud	Iran	51,7107	35,6395	1011	2387	V	73	403,4628	Endengered	0,6032	0,0038
Eyre Forest	New Zealand	168,2968	-45,4490	392	1838	III	790	0,7271	Vulnerable	0,8665	0,0177
Billiatt	Australia	140,4811	-34,9890	68	110	I	319	0,4686	Endengered	0,6995	0,0084
Mata Escura	Brazil	-41,0495	-16,3053	222	1099	I	1285	2,1987	Vulnerable	0,8933	0,0161
Shwesettaw	Myanmar	94,5460	20,2426	59	338	III	442	30,9044	Endengered	0,7437	0,0067
Kumbhalgarh	India	73,9038	24,5566	441	666	IV	203	117,7926	Endengered	0,7092	0,0037
Marojejy	Madagascar	49,7056	-14,4353	93	2057	II	1460	3,9391	Endengered	0,9252	0,0118
Loxahatchee	United States	-80,3321	26,5063	4	14	IV	103	3216,2880	Endengered	0,8549	0,0098
Goongarrie	Australia	121,5584	-29,9807	357	487	II	121	0,4084	Vulnerable	0,6503	0,0099
Corbett	India	78,9159	29,5898	320	1161	II	728	25,3539	Endengered	0,8647	0,0168
Tarumovskiy	Russia	46,6881	44,1325	-35	-4	IV	234	14,3111	Endengered	0,7604	0,0158
Catimbau	Brazil	-37,3469	-8,5034	442	1016	II	742	16,8379	Endengered	0,7722	0,0125
Barreira Branca	Brazil	-48,7642	-6,8122	128	252	V	1059	4,6786	Vulnerable	0,8737	0,0135
Krau	Malaysia	102,1760	3,7161	68	1982	IV	1287	44,7303	Stable	0,9076	0,0060
Dashtidzumsky	Tajikistan	70,1491	37,6054	657	2346	I	154	16,2266	Vulnerable	0,6521	0,0051
Veredas do Acari	Brazil	-45,4082	-15,6695	549	685	II	703	4,5493	Vulnerable	0,7728	0,0105
Maduru Oya	Sri Lanka	81,1775	7,5502	62	528	II	985	17,5375	Endengered	0,8607	0,0145
Chikmanskiy	Russia	81,2814	54,6573	170	203	IV	409	2,0078	Endengered	0,7006	0,0104
Mount Apo	Philippines	125,2905	6,9423	83	2804	II	97	493,7354	Endengered	0,7415	0,1243
Tamorpingla	India	82,8906	23,6853	353	796	IV	441	22,9712	Endengered	0,8154	0,0151
Mount Kei White Rhino	Uganda	31,1458	3,6880	849	1149	IV	860	10,3537	Endengered	0,8629	0,0097
Armstra Mountain	United States	-113,4233	34,3762	366	1244	I	102	2,7245	Endengered	0,6534	0,0070
Parque de la Montaña de Covadonga	Spain	-4,9075	43,2457	304	2549	II	624	2,0383	Endengered	0,7636	0,0405
Santa Izabel e Espalha	Brazil	-47,0460	-17,2000	593	959	V	899	3,5234	Endengered	0,8000	0,0133
Altacheyskiy	Russia	107,2376	50,9347	543	1303	IV	354	3,9221	Stable	0,7764	0,0342
Krivoklatsko	Czech Republic	13,8573	50,0009	246	585	V	495	60,1460	Endengered	0,8467	0,0161
Mallee Cliffs	Australia	142,6152	-34,2141	55	93	I	297	0,3119	Endengered	0,7061	0,0077
Chumbi Surla	Pakistan	72,3300	32,6700	475	960	IV	205	150,7257	Vulnerable	0,6883	0,0145
Askot Musk Deer	India	80,2747	29,6795	734	2329	IV	645	26,7631	Vulnerable	0,8451	0,0067
Karpatskiy	Ukraine	24,5834	48,2763	475	1885	II	590	6,3727	Vulnerable	0,8579	0,0107
Muara Kaman Sedulang	Indonesia	116,6910	0,1508	2	29	I	1252	2,1547	Endengered	0,8882	0,0073
Hingano-Arkharinskiy	Russia	130,7568	49,5486	140	526	IV	475	0,8621	Vulnerable	0,8203	0,0111
Cauvery	India	77,5695	12,1460	244	1350	IV	534	26,6500	Endengered	0,8112	0,0244
Overa-Aru	India	75,2556	34,1265	2070	4860	IV	191	26,0549	Vulnerable	0,6257	0,0381
Slavkovsky les	Czech Republic	12,7624	50,0723	391	948	V	573	26,4838	Endengered	0,8330	0,0119
Taganai	Russia	59,8460	55,3322	356	1056	II	413	64,6646	Endengered	0,8304	0,0099
Doi Pamnang	Thailand	99,0960	18,2931	308	1163	IV	654	13,4131	Stable	0,8500	0,0125

Protected Area	Country	Longitude	Latitude	Altitude min (m)	Altitude max (m)	IUCN Category (I-V)	Net Primary Productivity (g C m^{-2} y^{-1})	Human percent appropriation of NPP (%)	Global Conservation Ecosystem Status (Nature Serve G-Rank)	Mean NDVI Inside (0-1)	Std. NDVI Inside
Lwonde	Malawi	35,3351	-14,8671	468	783	II	753	47,4362	Stable	0,7662	0,0387
Manitagao Lake	Canada	-97,9938	51,3353	238	299	V	509	2,4279	Endengered	0,7629	0,0087
Etna	Italy	14,9722	37,7657	688	3241	V	73	581,5411	Vulnerable	0,7697	0,0443
Paytuna	Brazil	-54,2330	-2,1045	-1	220	V	907	1,1029	Endengered	0,7787	0,0767
Mom Ray	Viet Nam	107,6386	14,4873	266	1649	II	922	11,8994	Vulnerable	0,8619	0,0264
Maliau Basin	Malaysia	116,9005	4,8208	214	1721	I	1367	16,0631	Stable	0,9125	0,0155
Papikonda	India	81,5073	17,4292	22	709	IV	622	17,2885	Endengered	0,8632	0,0200
Sherengskiy	Russia	42,7665	61,6775	34	145	IV	328	3,8456	Vulnerable	0,8047	0,0112
Dhatigaon	India	77,9543	26,1525	202	369	IV	260	154,8055	Endengered	0,7026	0,0123
Prypyatskiy	Belarus	28,0414	51,9766	119	155	II	453	7,4424	Endengered	0,8161	0,0139
Cangandala/Malange	Angola	16,7269	-9,8724	1053	1164	II	899	1,8246	Endengered	0,8560	0,0045
Birskiy	Russia	134,6462	47,1890	75	1000	IV	471	1,2909	Vulnerable	0,8236	0,0048
Deux Bales	Burkina Faso	2,9437	11,6008	244	309	II	401	26,7183	Vulnerable	0,7290	0,0060
Région de Saül	French Guiyana	-53,2521	3,6908	142	715	IV	1378	0,0095	Stable	0,9093	0,0045
Arjan or Ajan and Parishan	Iran	51,9089	29,5838	798	2801	V	133	19,2708	Endengered	0,6283	0,0120
Bukit Socharto	Indonesia	116,9934	-0,8734	4	133	V	94	65,1817	Endengered	0,7904	0,0858
Aechisar	Ethiopia	37,8984	5,9919	1184	3072	II	939	29,9165	Vulnerable	0,8487	0,0142
Foz do Rio Santa Tereza	Brazil	-48,5824	-11,8749	230	290	V	883	0,7180	Vulnerable	0,8326	0,0118
Parc de la Mauricie	Canada	-72,9671	46,7884	140	443	II	549	82,5085	Endengered	0,8395	0,0105
Remdovskiy	Russia	27,8100	58,2563	27	75	IV	438	1,5921	Endengered	0,7831	0,0608
Chanata	Russia	44,7527	47,6279	-1	38	IV	165	4,4870	Endengered	0,6933	0,0120
Bogradskiy	Russia	90,6895	54,1665	443	958	IV	375	3,3999	Endengered	0,7333	0,0095
Ozyl-Tau	Kazakhstan	75,9999	50,2579	532	902	IV	148	1,9897	Endengered	0,6433	0,0036
Canon del Rio Blanco	Mexico	-97,2161	18,7916	790	2890	II	1014	16,2048	Endengered	0,7669	0,0407
Palma	India	86,3466	22,7279	81	814	IV	391	160,4027	Endengered	0,7805	0,0185
Oksky	Russia	40,7061	54,8131	90	137	I	434	7,6119	Endengered	0,8047	0,0201
Meana-Chaacha	Turkmenistan	60,5260	36,7170	243	998	IV	93	12,7627	Endengered	0,6534	0,0075
Tumenskiy	Russia	65,1171	57,5098	56	107	IV	414	7,0227	Endengered	0,7764	0,0097
Sitanadi	India	81,9540	20,1597	440	718	IV	531	18,7293	Endengered	0,8297	0,0176
Sary-Kolinskiy	Kazakhstan	62,4546	49,4231	89	151	IV	122	1,4567	Endengered	0,6296	0,0083
Taheceira do Rio das Balsas	Brazil	-46,7072	-9,2776	454	573	V	595	1,0706	Vulnerable	0,7724	0,0159
Bhoolpaneswar	India	73,7705	21,7533	23	734	IV	330	57,7972	Endengered	0,7439	0,0113
Sierra de Baza	Spain	-2,8155	37,3409	1017	2180	V	204	11,5855	Endengered	0,6999	0,0222
Buvubu	Burundi	30,3706	-3,1246	1350	1670	IV	716	41,2381	Endengered	0,8446	0,0073
Bairovskiy	Russia	72,9608	56,0922	91	115	IV	404	3,4319	Endengered	0,7028	0,0069
Kaieteur	Guyana	-59,6207	5,1726	76	1907	II	1407	0,0512	Stable	0,8741	0,0101
Rondane	Norway	9,8348	61,8838	910	1986	II	153	12,9569	Vulnerable	0,5898	0,0211
Tsasucheiskiy bor	Russia	115,0032	50,4581	604	712	IV	317	2,1087	Stable	0,6797	0,0164
Berezovyi	Russia	134,3411	43,8997	496	1461	IV	569	0,9384	Endengered	0,8325	0,0134
Mashpool	Australia	152,1667	-29,3496	245	1107	I	1319	0,2448	Endengered	0,8759	0,0189
Lebedinye ozera	Russia	108,1914	56,1336	424	1345	IV	300	0,6209	Stable	0,6889	0,0381
Bisotun	Iran	47,3044	34,4767	1288	3241	V	205	30,8052	Endengered	0,6363	0,0136
Cirente Velino	Italy	13,5640	42,1438	457	2283	V	586	20,4164	Endengered	0,7668	0,0510
Shambe	Sudan	30,7547	6,9465	397	431	II	860	2,3625	Vulnerable	0,8091	0,0239
Priangarskiy	Russia	103,5812	53,0731	389	616	IV	304	165,5199	Endengered	0,7386	0,0248
Elabuzhskiy	Russia	51,5898	55,7757	48	224	IV	317	9,2345	Endengered	0,7114	0,0101
Mulu	Malaysia	114,8903	4,0881	32	2185	II	1365	1,3733	Endengered	0,9063	0,0167
Gudremukh	India	75,1983	13,2179	58	1810	II	632	29,7786	Endengered	0,8618	0,0125
Narrow Hills	Canada	-104,6424	54,0904	448	693	II	435	0,1977	Endengered	0,7959	0,0162
Irane	Morocco	-5,1302	33,4318	1219	2065	V	452	5,1540	Endengered	0,7277	0,0217
Severo-Ayankinskiy listvennichnyi	Russia	166,5952	64,0044	85	823	IV	201	0,0414	Stable	0,6434	0,0083
Queyras	France	6,7833	44,7500	1107	3055	V	324	22,9229	Endengered	0,6843	0,0322
Catamá	Colombia	-76,1750	5,0628	243	4124	II	506	25,0944	Endengered	0,8136	0,0279
Bitnadoix River	Canada	-129,1607	54,1619	24	1927	II	257	2,7328	Endengered	0,6719	0,0839
Thingaza	Colombia	-73,6620	4,5469	1170	3827	II	342	14,0782	Stable	0,7822	0,0261
Zapadno-Altayskiy	Kazakhstan	83,7010	50,5213	663	1587	I	429	3,9349	Vulnerable	0,6763	0,0948
Adamello Brenta	Italy	10,7744	46,1747	707	3262	V	554	26,9723	Vulnerable	0,6635	0,1122
Sirsanovskiy	Kazakhstan	52,4697	51,4226	34	83	IV	323	5,4943	Endengered	0,7073	0,0155
Golden Ears	Canada	-122,4611	49,5134	80	1994	II	695	84,0311	Stable	0,7407	0,1093
Gondinskiy	Russia	113,3135	52,5310	916	1556	IV	318	2,1484	Stable	0,7231	0,0961
Bukit Barisan Selatan	Indonesia	98,4578	3,2459	410	1967	II	592	82,5993	Endengered	0,8823	0,0131
Nuble	Chile	-71,2957	-37,0757	1104	2767	IV	325	7,6107	Endengered	0,7139	0,0836

Table 1 con't. Complete dataset of the 114 protected areas (PA), including predictor and response variables used in statistical models and figures. PA isolation values in bold are areas which 95% confidence interval (C.I.) excludes zero.

Protected Area	Mean Contagion NDVI Inside (0-1)	Std. Contagion NDVI Inside	PA isolation 20 km In. - Out. Contagion (0-1)	PA isolation 20 km 5 % C.I.	PA isolation 20 km 95 % C.I.	PA isolation 10 km In. - Out. Contagion (0-1)	PA isolation 10 km 5 % C.I.	PA isolation 10 km 95 % C.I.	PA isolation 5 km In. - Out. Contagion (0-1)	PA isolation 5 km 5 % C.I.	PA isolation 5 k 95 % C.I.
Serra do Itajaí	0.7426	0,0515	**0,2325**	0.1849	0,2759	**0,0400**	0,0239	0,0529	0.0095	-0,0027	0,0228
El Rey	0,6555	0,0889	**0,2250**	0.1812	0,2615	**0,0422**	0,0201	0,0647	**0,0365**	0,0175	0,0561
Reserve del Bosque N	0,7727	0,1146	**0,2210**	0.1738	0,2627	**0,1436**	0,1415	0,1855	**0,0994**	0,0745	0,1276
Pico Bonito	0,6639	0,0851	**0,2189**	0.1665	0,2800	0,0271	-0,0078	0,0605	-0,0031	-0,0219	0,0209
Mount Kenya	0,6391	0,0776	**0,2003**	0.1583	0,2447	**0,0425**	0,0246	0,0590	**0,0229**	0,0015	0,0421
Eungella	0,6348	0,1160	**0,1901**	0.1419	0,2312	**0,0528**	0,0114	0,0879	0,0093	-0,0249	0,0353
Bromo Tengger Seme	0,6165	0,0897	**0,1874**	0.1441	0,2319	**0,0612**	0,0397	0,0795	**0,0451**	0,0282	0,0652
White Sands	0,8392	0,0817	**0,1872**	0.1269	0,2401	**0,0204**	0,0033	0,0399	-0,0022	-0,0217	0,0154
Khao Luang	0,5542	0,0364	**0,1862**	0.1442	0,2276	**0,0843**	0,0619	0,1009	**0,0345**	0,0243	0,0457
Zion	0,6662	0,0999	**0,1741**	0.1201	0,2184	**0,0680**	0,0325	0,0906	**0,0703**	0,0466	0,0930
Sadej Naikom	0,5592	0,0292	**0,1696**	0.1275	0,2020	**0,0677**	0,0459	0,0843	**0,0276**	0,0160	0,0417
Augrabies Falls	0,8534	0,1295	**0,1650**	0.1043	0,2124	-0,0061	-0,0364	0,0158	-0,0024	-0,0245	0,0240
Pu Huong	0,6147	0,0405	**0,1645**	0.1182	0,2048	**0,0191**	0,0057	0,0343	**0,0145**	0,0022	0,0243
Nanda Devi	0,6714	0,1638	**0,1631**	0.1159	0,2174	**0,0745**	0,0386	0,1164	0,0214	0,0158	0,0602
Swan Lake Kispiox R	0,4547	0,0333	**0,1601**	0.1254	0,2029	**0,0341**	0,0271	0,0433	**0,0226**	0,0160	0,0323
Jajrud	0,8430	0,0917	**0,1570**	0.1084	0,2136	**0,1478**	0,1425	0,2051	**0,0708**	0,0501	0,0932
Eyre Forest	0,5599	0,0654	**0,1545**	0.1054	0,1900	**0,0347**	0,0111	0,0595	0,0125	-0,0068	0,0283
Billiatt	0,6239	0,0315	**0,1516**	0.1058	0,1963	**0,0135**	0,0062	0,0237	-0,0030	-0,0112	0,0071
Mata Escura	0,5847	0,0739	**0,1513**	0.1165	0,2041	**0,0357**	0,0185	0,0523	**0,0303**	0,0104	0,0456
Shwesettaw	0,5199	0,0400	**0,1500**	0.1204	0,1894	**0,0212**	0,0084	0,0334	**0,0159**	0,0072	0,0249
Kumbhalgarh	0,5808	0,0195	**0,1499**	0.1145	0,1837	**0,0256**	0,0191	0,0319	**0,0249**	0,0180	0,0303
Marojejy	0,6809	0,1239	**0,1463**	0.0973	0,2047	0,0024	-0,0251	0,0241	-0,0004	-0,0255	0,0270
Loxahatchee	0,5524	0,0913	**0,1451**	0.1001	0,1828	**0,0530**	0,0328	0,0679	**0,0188**	0,0065	0,0402
Goongarrie	0,7925	0,0484	**0,1432**	0.0913	0,2001	**-0,0202**	-0,0317	-0,0114	-0,0031	-0,0152	0,0074
Corbett	0,5290	0,0636	**0,1412**	0.1107	0,1767	**0,0552**	0,0378	0,0730	**0,0344**	0,0196	0,0476
Tarumovskiy	0,5127	0,0679	**0,1408**	0.0977	0,1821	**0,0244**	0,0004	0,0472	-0,0119	-0,0288	0,0114
Catimbau	0,5120	0,0290	**0,1360**	0.1019	0,1737	**0,0334**	0,0249	0,0436	**0,0214**	0,0146	0,0290
Barreira Branca	0,5274	0,0584	**0,1330**	0.0961	0,1759	0,0123	-0,0052	0,0304	**0,0505**	0,0342	0,0738
Krau	0,5889	0,0530	**0,1323**	0.0876	0,1801	**0,0221**	0,0061	0,0356	0,0087	-0,0022	0,0208
Dashtidzumsky	0,5373	0,0514	**0,1317**	0.1041	0,1757	**0,0343**	0,0205	0,0514	**0,0424**	0,0286	0,0524
Veredas do Acari	0,5663	0,0311	**0,1303**	0.0975	0,1689	**0,0136**	0,0060	0,0220	-0,0061	-0,0125	0,0014
Maduru Oya	0,5519	0,0688	**0,1302**	0.0872	0,1615	0,0077	-0,0062	0,0229	0,0073	-0,0070	0,0209
Chikmanskiy	0,4758	0,0506	**0,1293**	0.1009	0,1674	**0,0307**	0,0198	0,0422	**0,0290**	0,0189	0,0398
Mount Apo	0,5230	0,1382	**0,1292**	0.0766	0,1851	**0,0405**	0,0109	0,0788	0,0253	-0,0132	0,0566
Tamorpingla	0,5152	0,0368	**0,1286**	0.0837	0,1558	**0,0159**	0,0065	0,0237	**0,0192**	0,0118	0,0272
Mount Kei White Rhi	0,5456	0,0283	**0,1284**	0.0933	0,1661	**0,0211**	0,0135	0,0265	**0,0190**	0,0137	0,0253
Arrastra Mountain	0,7199	0,0390	**0,1277**	0.0826	0,1827	-0,0270	-0,0423	0,0094	**-0,0153**	-0,0249	-0,0021
Parque de la Montaña	0,4466	0,0726	**0,1273**	0.0808	0,1647	**-0,0862**	-0,1055	-0,0681	**-0,0638**	-0,0821	-0,0449
Santa Izabel e Espalh	0,4858	0,0504	**0,1260**	0.0886	0,1568	0.0020	-0,0106	0,0138	-0,0109	-0,0216	0,0008
Altacheyskiy	0,4905	0,0468	**0,1256**	0.0893	0,1616	-0,0020	-0,0157	0,0122	0,0021	-0,0080	0,0158
Krivoklatsko	0,4501	0,0599	**0,1230**	0.0936	0,1551	**0,0489**	0,0351	0,0610	**0,0489**	0,0370	0,0616
Mallee Cliffs	0,6530	0,0621	**0,1227**	0.0786	0,1741	-0,0004	-0,0187	0,0115	0,0013	-0,0096	0,0161
Chumbi Surla	0,6051	0,0444	**0,1219**	0.0715	0,1615	-0,0155	-0,0256	0,0041	-0,0056	-0,0149	0,0044
Askot Musk Deer	0,4947	0,0232	**0,1188**	0.0903	0,1512	0,0064	-0,0014	0,0131	-0,0021	-0,0089	0,0035
Karpatskiy	0,4516	0,0432	**0,1170**	0.0869	0,1454	**0,0152**	0,0071	0,0249	0,0023	-0,0075	0,0135
Muara Kaman Sedula	0,5268	0,0378	**0,1165**	0.0901	0,1510	0,0002	-0,0106	0,0118	-0,0033	-0,0169	0,0121
Hingano-Arkharinskiy	0,4647	0,0307	**0,1160**	0.0902	0,1487	0,0018	-0,0034	0,0080	0,0049	-0,0010	0,0108
Cauvery	0,4579	0,0410	**0,1147**	0.0773	0,1560	-0,0091	-0,0186	0,0004	0,0005	-0,0082	0,0085
Overa-Aru	0,4910	0,1015	**0,1131**	0.0666	0,1519	-0,0016	-0,0354	0,0243	0,0075	-0,0181	0,0396
Slavkovsky les	0,4554	0,0393	**0,1130**	0.0863	0,1441	**0,0398**	0,0305	0,0482	**0,0294**	0,0215	0,0392
Taganai	0,4286	0,0396	**0,1116**	0.0883	0,1398	**0,0300**	0,0220	0,0416	0,0042	-0,0031	0,0141
Doi Pamuang	0,4855	0,0256	**0,1115**	0.0811	0,1473	**0,0128**	0,0070	0,0167	**0,0111**	0,0071	0,0191

Protected Area	Mean Contagion NDVI Inside (0-1)	Std. Contagion NDVI Inside	PA isolation 20 km In. - Out. Contagion (0-1)	PA isolation 20 km 5 % C.I.	PA isolation 20 km 95 % C.I.	PA isolation 10 km In. - Out. Contagion (0-1)	PA isolation 10 km 5 % C.I.	PA isolation 10 km 95 % C.I.	PA isolation 5 km In. - Out. Contagion (0-1)	PA isolation 5 km 5 % C.I.	A isolation 5 k 95 % C.I.
Liwonde	0,5034	0,0240	**0,1105**	0,0727	0,1535	**0,0165**	0,0054	0,0269	0,0152	-0,0017	0,0117
Mantagao Lake	0,4257	0,0303	**0,1098**	0,0802	0,1401	**0,0122**	0,0040	0,0198	0,0229	0,0137	0,0291
Etna	0,4479	0,0857	**0,1073**	0,0771	0,1518	-0,0030	-0,0354	0,0218	-0,0356	-0,0711	-0,0420
Paytuna	0,4567	0,1218	**0,1069**	0,0698	0,1480	0,0082	-0,0153	0,0368	0,0222	-0,0134	0,0494
Mom Ray	0,5389	0,0943	**0,1066**	0,0659	0,1520	0,0178	-0,0023	0,0389	0,0194	0,0003	0,0406
Maliau Basin	0,6139	0,1158	**0,1064**	0,0553	0,1483	**-0,0440**	-0,0723	-0,0196	**-0,0367**	-0,0669	-0,0026
Papikonda	0,4926	0,0690	**0,1062**	0,0746	0,1418	0,0017	-0,0107	0,0183	-0,0097	-0,0248	0,0058
Sherengskiy	0,4159	0,0325	**0,1061**	0,0771	0,1343	**0,0092**	0,0002	0,0197	**0,0099**	0,0021	0,0167
Ghatigaon	0,5194	0,0373	**0,1057**	0,0721	0,1404	-0,0024	-0,0100	0,0063	-0,0038	-0,0124	0,0046
Prypyatskiy	0,4472	0,0470	**0,1044**	0,0773	0,1268	**0,0127**	0,0020	0,0237	**0,0153**	0,0025	0,0274
Kangandala/Malange	0,4924	0,0226	**0,1044**	0,0692	0,1367	0,0001	-0,0067	0,0058	-0,0011	-0,0091	0,0043
Birskiy	0,4753	0,0212	**0,1037**	0,0741	0,1389	**-0,0173**	-0,0241	-0,0106	**-0,0147**	-0,0215	-0,0101
Deux Bales	0,5510	0,0234	**0,1034**	0,0658	0,1481	**-0,0139**	-0,0209	-0,0064	-0,0215	-0,0263	-0,0137
Région de Saul	0,5384	0,0414	**0,1033**	0,0690	0,1447	0,0064	-0,0015	0,0174	0,0028	-0,0087	0,0149
Arjan or Ajan and Pa	0,6783	0,1172	**0,1032**	0,0533	0,1527	**-0,0623**	-0,0905	-0,0435	-0,0343	-0,0576	0,0040
Bukit Soeharto	0,4202	0,1147	**0,1029**	0,0611	0,1430	0,0277	-0,0024	0,0552	**0,0447**	0,0168	0,0661
Nechisar	0,4868	0,0414	**0,1013**	0,0654	0,1315	-0,0110	-0,0245	0,0004	**-0,0130**	-0,0254	-0,0027
Foz do Rio Santa Ter	0,5077	0,0469	**0,1012**	0,0560	0,1322	-0,0015	-0,0106	0,0088	0,0031	-0,0067	0,0114
Parc de la Maurete	0,4393	0,0403	**0,0997**	0,0754	0,1321	0,0008	-0,0098	0,0087	-0,0035	-0,0108	0,0101
Remdovskiy	0,4121	0,0783	**0,0996**	0,0719	0,1305	**0,0399**	0,0229	0,0558	**0,0275**	0,0098	0,0440
Khanata	0,5229	0,0622	**0,0988**	0,0635	0,1404	-0,0142	-0,0290	0,0046	**-0,0207**	-0,0380	-0,0076
Bogradskiy	0,4157	0,0280	**0,0979**	0,0674	0,1284	-0,0007	-0,0055	0,0052	0,0000	-0,0050	0,0059
Kzyl-Tau	0,5454	0,0399	**0,0969**	0,0595	0,1339	**0,0103**	0,0011	0,0198	**0,0104**	0,0058	0,0285
Canon del Rio Blanco	0,5504	0,0780	**0,0967**	0,0415	0,1382	**-0,0286**	-0,0477	-0,0107	**-0,0284**	-0,0481	-0,0124
Dalma	0,4907	0,0358	**0,0960**	0,0549	0,1284	**-0,0226**	-0,0298	-0,0138	**-0,0054**	-0,0152	0,0022
Oksky	0,4167	0,0345	**0,0954**	0,0737	0,1252	**0,0097**	0,0003	0,0177	**0,0088**	0,0014	0,0172
Meana-Chaacha	0,6184	0,0356	**0,0948**	0,0565	0,1466	**-0,0464**	-0,0572	-0,0359	**-0,0179**	-0,0280	-0,0086
Tjumenskiy	0,4019	0,0301	**0,0946**	0,0648	0,1201	-0,0112	-0,0197	0,0019	0,0025	-0,0053	0,0089
Sitanadi	0,4804	0,0438	**0,0940**	0,0548	0,1322	-0,0140	-0,0232	0,0064	-0,0081	-0,0181	0,0013
Sary-Kolinskiy	0,5535	0,0725	**0,0937**	0,0529	0,1309	**-0,0682**	-0,0834	-0,0547	**-0,0608**	-0,0737	-0,0474
Cabeceira do Rio das	0,4738	0,0373	**0,0936**	0,0541	0,1240	**-0,0586**	-0,0662	-0,0495	**-0,0338**	-0,0423	-0,0228
Shoolpaneswar	0,4998	0,0479	**0,0927**	0,0512	0,1286	**-0,0146**	-0,0258	-0,0048	0,0026	-0,0077	0,0204
Sierra de Baza	0,6262	0,0732	**0,0904**	0,0449	0,1459	**-0,0700**	-0,0886	-0,0382	**-0,0643**	-0,0831	-0,0453
Ruvubu	0,5071	0,0320	**0,0901**	0,0616	0,1334	**-0,0163**	-0,0229	-0,0100	**-0,0075**	-0,0147	-0,0019
Barrovskiy	0,4366	0,0322	**0,0865**	0,0596	0,1197	-0,0044	-0,0123	0,0015	-0,0042	-0,0138	0,0061
Kaieteur	0,4407	0,0435	**0,0853**	0,0483	0,1248	**-0,0267**	-0,0382	-0,0143	**-0,0164**	-0,0260	-0,0020
Rondane	0,3769	0,0603	**0,0826**	0,0557	0,1074	-0,0004	-0,0100	0,0124	-0,0058	-0,0203	0,0119
Tsasucheiskiy bor	0,4655	0,0332	**0,0823**	0,0519	0,1158	**-0,0278**	-0,0347	-0,0190	**-0,0204**	-0,0286	-0,0123
Berezovyi	0,4725	0,0433	**0,0819**	0,0459	0,1212	**-0,0113**	-0,0217	-0,0029	-0,0044	-0,0127	0,0047
Washpool	0,6378	0,0908	**0,0808**	0,0426	0,1397	**-0,0414**	-0,0606	-0,0206	-0,0121	-0,0049	0,0356
Lebedinye ozera	0,3819	0,0499	**0,0799**	0,0522	0,1060	-0,0045	-0,0159	0,0058	**-0,0178**	-0,0286	-0,0067
Bisotun	0,5873	0,0498	**0,0798**	0,0447	0,1327	**-0,0742**	-0,0823	-0,0620	**-0,0409**	-0,0548	-0,0267
Sirente - Velino	0,4255	0,0779	**0,0794**	0,0437	0,1225	**-0,0428**	-0,0598	-0,0279	**-0,0481**	-0,0627	-0,0351
Shambe	0,5190	0,0649	**0,0789**	0,0464	0,1278	**-0,0427**	-0,0585	-0,0280	**-0,0433**	-0,0589	-0,0261
Priangarskiy	0,3777	0,0307	**0,0779**	0,0589	0,1037	**0,0096**	0,0009	0,0174	-0,0093	-0,0171	0,0020
Elabuzhskiy	0,3896	0,0277	**0,0770**	0,0511	0,1016	**0,0095**	0,0029	0,0153	0,0027	-0,0039	0,0095
Mulu	0,6091	0,1610	**0,0761**	0,0111	0,1150	**-0,0756**	-0,1036	-0,0442	**-0,0741**	-0,1032	-0,0302
Kudremukh	0,4926	0,0591	**0,0711**	0,0396	0,1185	**-0,0545**	-0,0675	0,0418	**-0,0495**	-0,0884	-0,0330
Narrow Hills	0,4247	0,0423	**0,0708**	0,0443	0,1019	-0,0201	-0,0308	0,0079	**-0,0172**	-0,0266	-0,0084
Ifrane	0,5306	0,0735	0,0694	-0,0093	0,1156	**-0,0886**	-0,1262	-0,0870	**-0,0713**	-0,0932	-0,0539
Severo-Ayankinskiy I	0,4442	0,0440	**0,0676**	0,0313	0,0994	-0,0147	-0,0253	0,0018	-0,0072	-0,0126	0,0077
Queyras	0,3815	0,0483	**0,0673**	0,0351	0,0993	-0,0026	-0,0194	0,0121	0,0057	-0,0136	0,0257
Tatamá	0,3824	0,0797	0,0667	-0,0104	0,1260	-0,0069	-0,0299	0,0090	-0,0104	-0,0275	0,0052
Gitnadoix River	0,2979	0,0818	0,0653	-0,0149	0,0928	**-0,0432**	-0,0634	-0,0288	**-0,0301**	-0,0466	-0,0145
Chingaza	0,3720	0,0356	**0,0643**	0,0102	0,1003	**-0,0394**	-0,0533	-0,0282	**-0,0250**	-0,0371	-0,0152
Zapadno-Altayskiy	0,3592	0,1217	**0,0607**	0,0222	0,0956	**-0,0379**	-0,0611	-0,0172	**-0,0345**	-0,0564	-0,0193
Adamello Brenta	0,3578	0,1426	**0,0605**	0,0146	0,0999	-0,0086	-0,0508	0,0355	-0,0166	-0,0377	0,0245
Kirsanovskiy	0,4419	0,0506	**0,0596**	0,0272	0,0922	**-0,0349**	-0,0448	-0,0261	**-0,0361**	-0,0494	-0,0221
Golden Ears	0,3967	0,1612	**0,0550**	0,0175	0,1037	-0,0298	-0,0678	0,0137	-0,0152	-0,0557	0,0193
Kondinskiy	0,4462	0,0174	**0,0536**	0,0329	0,0827	**0,0146**	0,0097	0,0196	0,0040	-0,0001	0,0086
Bukit Barisan Selatan	0,5354	0,0799	**0,0493**	0,0014	0,0823	**-0,0455**	-0,0676	-0,0265	**-0,0314**	-0,0476	-0,0066
Ñuble	0,3765	0,1156	0,0427	-0,0069	0,0733	**-0,0915**	-0,1424	-0,0834	**-0,0442**	-0,0718	-0,0131

Table 2. Best regression models of protected area isolation for different buffer distances: 10-20 km, 5-10 km, and 0-5 km on the coefficient of variation of NDVI inside the protected areas (CV NDVI), % human appropriation of net primary productivity (% HANPP, log-transformed) outside the protected areas, and IUCN management status (i.e., low-protection and high-protection status). Global Moran's autocorrelation coefficient *I* for model residuals indicate that residuals are not spatially patterned.

Response	Predictor	t	p	Full model R^2adj*	Moran's *I* (model residuals)
Isolation 10-20 km	log CV NDVI	-4.258	< 0.001		
	log % HANPP	1.406	0.163	0.24	-0.0201
	IUCN level	-3.929	< 0.001		
Isolation 5-10 km	log CV NDVI	-3.359	0.001		
	log % HANPP	2.695	0.008	0.12	-0.0217
	IUCN level	-1.718	0.088		
Isolation 0-5 km	log CV NDVI	-2.860	0.005	0.08	0.0074
	log % HANPP	1.355	0.178		

*Adjusted coefficient of determination

CONCLUSION GÉNÉRALE

The novel metric (i.e. difference in mean NDVI contagion) developed and presented here offers a novel way to quantify PA isolation rapidly at the global scale and independent of ecosystem type or socioeconomic setting. Contagion describes spatial-temporal patterns of LVH and our application of it here indicates that there is a significant level of contrast in these patterns (i.e. isolation) between PA's and their immediate surroundings. This discontinuity occurred in nearly all of the PAs analyzed. Isolation resulted from either their placement in the landscape (i.e. some level of 'natural' biophysical isolation) or landcover alteration outside their borders likely due to increased human land use and fragmentation of the vegetation matrix.

The contagion metric based on spatiotemporal NDVI maps expands on the two previous studies quantifying PA isolation at broad scales (c.f., DeFries et al. 2005; Joppa et al. 2008). In contrast to previous studies, our isolation metric is not a binary measure of tree cover limited to forest-dominated ecosystems (i.e., a measure of the percentage of forested land based on a 0 or 1 pixel value of forest cover), but can be applied and is comparable across a broader range of biomes and ecoregions. It is, therefore, not limited to forest dominated systems or reliant on coarse land classification products. In fact, our metric sometimes produced very different isolation values than those based on tree cover classifications (e.g. the PA Serra do Itaja, Brazil as discussed in Chapter 1). The ability to capture discontinuity in the landcover vegetation patterns with increasing distance from the PA's border might have been overlooked by previous measures of PA isolation. Nonetheless, in regions where PAs are not surrounded by other reserves, the results presented through this project are in general agreement with the two previous studies that measured some form of PA isolation (c.f., Joppa et al. 2008 and DeFries et al. 2005). That is, the

overwhelming majority of PAs analyzed are becoming increasingly isolated from their surroundings. Our analysis further indicates that this isolation is widespread across ecoregions and protection status of the world's PA network.

PA isolation may not only be widespread and at risk of increasing, but isolation may be a diffusive process, invading towards the PA through time. Isolation occurs while internal influences appear also to extend beyond the reserve border and into nearby unprotected lands to some extent (0 -10 km from the border). This would also explain why the difference in mean contagion was largest when calculated based on the buffer farthest from the PA. These findings are also further explained by the fact that the positive relationship between HANPP and PA isolation was stronger in low protection areas, which are located closer to centres of human activities (i.e., at lower altitudes and in regions of higher NPP and population densities; Hansen & Rotella, 2002). PA and human density (based on a 1 km resolution gridded human population data product, but results not presented here), in fact, shared nearly the identical relationship as described between PA isolation and HANPP (Fig. 3). Thus, this indicates that human population growth, as well as land development, may be increasing around, and invading towards PAs, especially low protection ones.

The mean difference in contagion metric has the ability to capture key habitat features and changes in those features across a landscape independent of the cause (e.g. clear cutting of forest, alternative cutting systems, burning, agriculture, urbanization) or ecosystem type since it is based on the spatial-temporal patterns of NDVI. Of course our metric is not free from limitations. The generality of our approach has a price in that, without supplementary information, it cannot be explicitly related to the environmental and socio-economic processes (e.g. forestry, agriculture, urbanization, geography) modifying the landscape pattern around PAs. Moreover, we have not yet used such explicit measures of landcover alteration to calibrate the isolation metric and define benchmarks for "high" isolation vs "low" isolation values. Further

application of the isolation metric with incorporation of landcover/landuse categorical maps for PAs and their surroundings will help define what landscape processes generate the highest PA isolation values to set such benchmarks.

Not only did we find significant differences in mean contagion between inside PAs and their surroundings, but isolation was highest for high-protection status reserves. This seems to be true irrespective of human population densities and HANPP. Moreover, parks of the highest protection status (IUCN I & II) tend to have lower human population densities nearby than low-protection ones (i.e. they are remote). However, this does not suggest an absence of human induced landcover alterations outside high-protection areas, but that these effects, if present, are minimal or were not identified by our analysis. Joppa et al. (2008) found little change in % of natural forest cover between PAs and their surroundings for most reserves in the Congo and Amazon regions, concluding these remote parks are protected 'de facto' (i.e. they are protected simply by their remote setting). As they state, the effects of such parks designations as reserves may be negligible and a more fine-scale analysis of whether these PAs do better by some metric than unprotected lands would be required to comment on their value as such. However, what our analysis discloses is that even remote, high protection, PAs may be isolated. Granted, natural forms of isolation, which are essentially due to a biased geographic placement of the reserve, are not necessarily expected to translate into losses of biodiversity and ecological integrity within PAs. However, potential negative effects on biodiversity and ecological integrity, due to an intensification of human activities in the neighbouring lands, could be predicted to happen much more rapidly in PAs which are naturally presenting higher degree of isolation.

Thus it appears that inside vs. outside differences in mean contagion between high and low-protection PAs are influenced by the combination of their geographic placement and the management practices associated with their IUCN protection status. If we consider PA isolation a significant threat to their

efficacy at conserving biodiversity our results raise an alarming feature perhaps representative of the global PA network. Namely, reserves that we deem most valuable and capable in the preservation of biodiversity and ecosystem functions, high-protection areas, are also those which are most highly contrasted with their surroundings. This is because high-protection areas are successful in maintaining their inside patterns of vegetation cover, yet they are often placed in geographically isolated settings, or in more remote regions where intensification of human activities outside their borders can only increase. The situation is no better for low protection areas, since they are often not so successful in maintaining the integrity of the vegetation cover inside their borders, and are concurrently impacted by landcover alterations outside. These two points emphasize the challenge we face in planning an effective PA network, a necessity for the conservation of the globe's biodiversity since PAs are the cornerstone of this effort. The PA isolation metric presented here offers a novel tool to assist this conservation effort.

A key management implication from these results for low-protection reserves may be to direct conservation efforts at achieving a balance between maintaining natural LVH inside the reserves, while protecting similar features in the surrounding lands under increasing human density related factors of landcover alteration. If PAs of these types are to be effective at eliminating species losses inside their borders, this may equate to both an increase on the strictness and type of resource use inside their borders and integrative management of surrounding lands. On the other hand, if low protection areas are not mandated to maintain ecological integrity and species populations, but only for some recreational activities or natural monuments, the degree of isolation or maintenance of inside PA cover pattern may not be important. However, the ICUN category definitions and the general view in related literature is that PA's main function, regardless of their IUCN rank, is to

maintain the biodiversity and ecological functions of their region. Thus, the level of isolation and its causes in these areas must be addressed.

Perhaps more importantly, attention must also be drawn towards how much high-protection reserve's surroundings are being converted to non-natural vegetation types due to resource extraction not necessarily linked to human population density (i.e. agriculture and forestry practices). Special attention in these PAs, which may be primarily isolated by variations in cover pattern due to natural features, must be directed at the intensification of human activities in the neighbouring lands. The potential negative effects on biodiversity and ecological integrity could be predicted to happen much more rapidly in PAs which are already naturally presenting higher degrees of isolation. This brings to light another key management and planning issue for the PA network as a whole. That is, the rethinking of where PA boundaries are established and ensuring the maintenance of natural LVH outside them (i.e. keeping them remote), or at least designing integrative management measures to ensure the adequate maintenance of natural vegetation cover outside these PA borders. Of course this requires defining what an adequate level of outside habitat is needed to ensure the maintenance of local populations. This is undoubtedly a complex and large task, but one that is necessary and possible through integrating analytical techniques, such as the one presented here, the vast amount of species and spatial landcover datasets becoming ever-available and the management policies of the PA network.

A key issue for conservation is the question of how PA isolation translates into a loss of biodiversity and ecological integrity. While we have not empirically addressed this question here we suggest that our application has such potential. The relationship between PA isolation and HANPP for PAs located in endangered ecoregions (Fig. 4) indicated that the ecoregion vulnerability status of a PA is linked to its degree of isolation, but only in regions classified as endangered. This relationship may suggest that high isolation translates into a

loss of ecological integrity because the conservation status of an ecoregion depends largely on the number of threatened species in the region and many, if not most, of an ecoregion's taxa are likely to be found in PAs. A bulk of research would also suggest that PA isolation, as measured by our novel metric, compromises their ecological integrity (e.g. species populations and ecological functions) (Fairbanks & McGwire 2004; Gillespie et al. 2008; Gould 2000; Lassau & Hochuli 2008). These studies highlight the importance of preserving natural vegetation heterogeneity and the structural features of the landcover matrix for the maintenance of ecological integrity and biodiversity.

Both human population densities and land use are expanding and intensifying rapidly in the unprotected wild and semi-wild lands surrounding many of the world's PAs (Hansen and Rotella 2002; Hansen and DeFries 2007; Wittemyer et al. 2008). This landuse intensification is likely isolating PAs and has significant implications to the ecological integrity and efficacy of PAs. The novel contagion contrast metric presented here offers a new way to quantify PA isolation and, unlike previous analyses, it achieves this on a global scale independent of PA management category, ecoregion or socioeconomic setting. The loss of conservation capacity in protected areas, in the form of the discontinuity in habitat features with increasing distance from their boundaries, also underscores the critical conservation value of remaining large tracts of natural vegetation cover and the need to protect land cover representative of the generalized region as opposed to rare and biophysically isolated habitats. Moreover, the prevalence of PA isolation by our metric, emphasizes the urgent need to acknowledge the biased placement of PAs towards devalued lands and shift policy and conservation focus from simple reserve area coverage and percentage-based targets to integrative management and protection of lands surrounding reserves.

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